FOOD HABITS, VOCALIZATIONS, AND TERRITORIALITY OF ALASKAN RED SQUIRRELS (G. TAMIASCIURUS)

A

THESIS

Presented to the Faculty of the
University of Alaska in Partial Fulfillment
of the Requirements
for the Degree of
MASTER OF SCIENCE

By
Frances A. Nodler, B.A.
College, Alaska
May, 1973

FOOD HABITS, VOCALIZATIONS, AND TERRITORIALITY OF ALASKAN RED SQUIRRELS (G. TAMIASCIURUS)

RECOMMENDED:

Robert B. Weeden by JCQ

Peter C. Lent

Frederick C. Dean
Chairman

Frederick C. Dean
Department Head

APPROVED:

Frederick C. Dean
Dean of the College of Biological Sciences

11 May 1973
Date

Vice President for Research and Advanced Study

14 May 1973
Date

ABSTRACT

Observations were made of two red squirrel (Tamiasciurus hudsonicus) populations during the year of 1971, near Fairbanks, Alaska.

Squirrels in the field readily utilized black spruce cones when the preferred white spruce was not available. Evidence suggests that adults disproportionately controlled middens with higher food supplies. Juveniles made up a disproportionate number of the squirrels which cached no cones in 1971.

Seven vocalizations were distinguished in the field; the territorial call, the alarm call, the offensive threat call, the defensive threat call, and three appeasement calls.

The squirrels under observation controlled year round territories. Territorial behavior, including chases, boundary disputes, and fights between trapped and free squirrels were observed. In two cases, territorial squirrels were unable to drive invading squirrels from their territories, but no permanent shifts in territorial ownership caused by intraspecific aggression were observed. At the time of dispersal of juvenile squirrels, the mothers of three families abandoned their own territories and remained in loose association with their young until or shortly before the young established their territories. High population pressures and low food supplies may have caused this unusual behavior.

ACKNOWLEDGMENTS

The author gratefully acknowledges the assistance of the following people:

Dr. Frederick C. Dean, Head, Department of Wildlife and Fisheries, for his suggestions concerning all aspects of the study, for critically reading the manuscript, and for his enthusiasm concerning red squirrels.

Dr. Peter C. Lent, Assistant Leader, Alaska Cooperative Wildlife Research Unit, and Dr. Robert B. Weeden, Professor of Wildlife and Fisheries, for critically reading the manuscript and providing many helpful suggestions.

John Zasada, Silviculturist, U. S. Forest Service, Institute of Northern Forestry, for sharing his time and knowledge of white spruce seed production. Roy Beckwith, Principal Entomologist, and Richard Barney, Principal Fire Control Scientist, of the U. S. Forest Service, Institute of Northern Forestry, for providing transportation to the Bonanza Creek study area. Mrs. Elizabeth Berry and Jerry Wolff for their amiable companionship during the many hours spent on the road.

Special thanks to Gordon and Marilyn Herreid for the use of their land for the Ballaine Road study area.

Robert C. Pelz, for his expertise with a camera, for patient assistance in the field, and for his technical help in the production of the sound spectrographs.

Mrs. Carol Callahan, for typing and proofreading the final copy of the thesis.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

This is the sixth of a series of ecological studies of the red squirrel, Tamiasciurus hudsonicus preblei[1], in interior Alaska. The relationship of the red squirrel to its food supply, population dynamics, and reproduction have been studied by Brink (1964), M.C. Smith (1967), Streubel (1968), Krasnowski (1969), and Modafferi (1972).

The major emphasis of the present study has been placed upon territorial behavior because of its importance in relation to food supply and population dynamics. C. C. Smith's (1968) discussion of social behavior in the genus Tamiasciurus has laid the foundation for much of the work. Since acoustic signals are frequently emitted during interactions between red squirrels, observations of the behavioral context of vocalizations added greatly to the understanding of territorial behavior. Many previous workers have encountered difficulties in interpreting observations of squirrel behavior, particularly interactions among individuals. This has been largely due to lack of information about the age, sex, or past

[1]Scientific names of mammals follow Hall and Kelson (1959), those of birds follow the 1957 check-list of the American Ornithologists' Union, and those of trees and shrubs follow Viereck and Little (1972).

history of the squirrels involved. During the present study, an intensive program of live-trapping and tagging has supplied the needed information, facilitating interpretation of behavioral observations.

Information on food habits and population density has been included in the present study to provide data related to the long term goals of the red squirrel studies in interior Alaska.

The study was sponsored by a National Science Foundation Graduate Traineeship (NSF GZ-1535) and the Department of Wildlife and Fisheries, University of Alaska, College, Alaska.

STUDY AREAS

Bonanza Creek Experimental Forest

The Bonanza Creek Experimental Forest is located about 25 km southwest of College, Alaska. It occupies the northeast quarter of T 1N, R 4W of the Fairbanks Meridian. Trapping, tagging, and observations were confined to a 457-m square (21-ha) grid, previously established by M. C. Smith (1968). The grid is on a steep, south-facing slope with an average elevation of 305 m above sea level. White spruce, Picea glauca is the dominant species on the study area (M. C. Smith, 1968). Quaking aspen, Populus tremuloides, American green alder, Alnus crispa, and paper birch, Betula papyrifera, are common (M. C. Smith, 1968). Black spruce, Picea mariana is present but rare. M. C. Smith (1967) presents a detailed description of the study area, including lists of plant, bird, and mammal species which occur there.

Ballaine Road Study Area

This study area is located east of Ballaine Road and north of Herreid Drive approximately 4 km northwest of College, Alaska. It occupies the southeast quarter of section 19 T 1N, R 1W of the Fairbanks Meridian. An area of 19 ha was intensively studied (see Fig. 3), but some field work was done on adjacent areas. Unlike the Bonanza Creek grid, the land is gently sloping, low (average

elevation of 204 m above sea level), and poorly drained. The vegetation is heterogeneous in comparison with that at Bonanza Creek. The white spruce trees are mostly located on slightly elevated ground, and the canopy is less dense than at Bonanza Creek. Also in contrast to Bonanza Creek, black spruce is abundant at Ballaine Road. It occurs at the edges of the white spruce groves in the slightly wetter areas. These black spruce trees provide an important food source for red squirrels when the white spruce cone crop fails.

The permanent residence of humans at the Ballaine Road study area is another important factor. Although only one dwelling is located directly on the area of intensive study, there are several houses in the immediate vicinity. Garbage cans and bird feeders provide an additional, often high quality food source. Humans and their domestic dogs are red squirrel predators that are absent at Bonanza Creek.

Because of the heterogeneous nature of the Ballaine Road study area, the area of habitat usable by red squirrels was determined by the following method. The negative of an aerial photograph was projected onto a piece of graph paper (20 squares per inch), and detailed outlines of the usable habitat, spruce groves and large isolated trees, were carefully drawn. The number of squares covered by

usable habitat was divided by the number of squares of the whole study area. The resulting quotient represented the percentage of the study area covered by usable habitat for red squirrels. This value was calculated as about 29% of the study area.

METHODS

Live-trapping and Tagging

General observations were begun at the Ballaine Road study area in January, 1971. Intensive trapping and tagging were initiated here on April 1 and continued through December, 1971. A few observations were made in the spring and early summer of 1972. Field work was initiated on the Bonanza Creek study area in June, 1971, and was suspended in December, 1971.

An attempt was made to trap and tag every squirrel on each study area. National brand live traps were placed directly on the middens. These were baited with peanut butter and rolled oats. Traps usually were checked every 2 or 3 hours and were never left set overnight. A trout net was used to restrain squirrels during handling. As shown in Figure 1, the net was held in front of the door of the trap. After a slight hesitation, the squirrels would run into the net and become entangled. They were further restrained by grasping them around the shoulders with a gloved hand. The net proved to be extremely satisfactory. It provided little protection for the handler, but provided more flexibility for tagging and taking measurements than a wire restraining cone would offer.

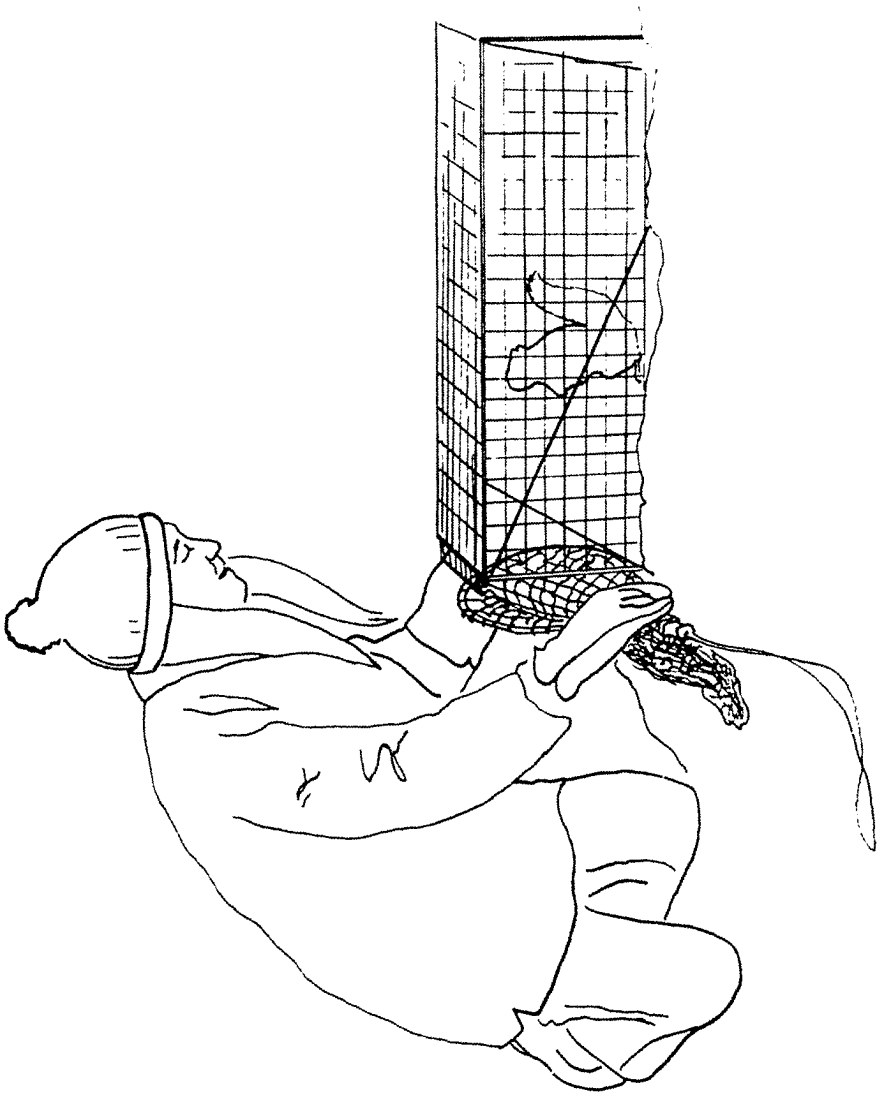

Figure 1. Removal of squirrel from live trap with the use of a trout net.

A serially numbered, number one monel fingerling tag was attached to each ear. Loops of colored polyvinyl chloride plastic tubing were also attached to the ears using the method described by Krasnowski (1969), except that the tubing was tied with a square knot and was not sealed with acetone. "Nyanzol A" dye was prepared and applied as described by Fitzwater (1941). The dye, placed in various patterns on the fur, and the colored ear loops permitted identification of each squirrel from a distance of approximately 20 m with the aid of binoculars. Information collected for each squirrel included age, sex, weight, date, time, and location. Late in the season, young of year became indistinguishable from adults, and age could not be determined by field techniques. Measurements of total length, tail, hind foot, and ear were recorded. Vocalizations and other behavioral observations were noted. All trapped animals were released after tagging or identification. Attempts were made to keep conditions on both study areas as natural as possible. Each free squirrel sighted was identified, if tagged. The location of the squirrel, as well as vocalizations emitted and other behavioral observations were noted.

Population Density

Population density was determined by counting the number of active middens, following the principle of one

squirrel per active midden as discussed by M. C. Smith (1968), except in cases where auxiliary middens were positively identified. The program of live-trapping, tagging, and resighting facilitated identification of auxiliary middens.

Food Habits

During the first two weeks of August, 1971, at Bonanza Creek, 28 middens were partially excavated to obtain a rough estimate of the relative amounts of cones still remaining from the harvest of 1970. On the basis of the relative amounts of cones, the middens were ranked as high, high-medium, medium, low, and very low. They ranged from those containing an abundance of cones to those in which no cones could be found.

During the autumn of 1971 the middens on both study areas were watched closely to obtain an estimate of the amounts of cones cached. Fortunately, red squirrels temporarily store cones in piles on top of the middens before burying them. Each pile was marked so that it was not recounted on subsequent visits. If new cones had obviously been added to the pile, the amount or number of cones was reestimated. The amounts of cones cached at Bonanza Creek fell into five groupings, with no overlap. These were: 35-70 liters (about 1-2 bushels), 15-20 liters (about 0.4-0.6 bushel), 500-1,000 cones, fewer than 200 cones,

and no evidence of cone caching. There are approximately 140 white spruce cones per liter, or about 5,000 cones per bushel.

In the early phases of the field work, it became apparent that a complete cone crop failure in the autumn of 1971 would leave only two sources of cones for the fall harvest. These would be cones raided from neighboring middens, and cones on the ground which had been cut the previous year but not retrieved and cached. Although white spruce cones open and close with changes in the humidity, it was felt that some of the cones which had fallen into moist depressions and under the shade of logs would retain sound seed. Cone samples were collected to determine the selectivity exercized by the squirrels when caching cones. In early August, before caching had begun, a sample of unopened cones which had been cut but not cached the previous year was collected from the ground on squares 1-10 of the Bonanza Creek grid. Only those cones which had fallen into moist depressions and thus most likely to retain seed were chosen. In November, cone samples were collected from newly cached piles on middens 17E and 25W, controlled respectively by an adult female and an adult male. Fifty of the cones collected from the ground were analysed for percentage of cones containing filled seed, as well as for the percentage of filled

seed in the productive zone of the cones. Twenty-five cones from each of the samples collected from the middens were selected at random and subjected to the same analysis.

The cone crop rating system used for this study was that developed by Werner (1964) and described by Zasada and Viereck (1970) as follows:

1. No cones on any trees
2. Few cones on occasional trees
3. Few cones on 25 per cent of trees
4. Few cones on 25 per cent of trees--many cones on occasional trees
5. Few cones on 75 per cent of trees
6. Few cones on 75 per cent of trees--many cones on some trees
7. Some cones on all trees
8. Many cones on some trees--some cones on all trees
9. Many cones on 75 per cent of trees--some cones on all trees
10. Many cones on all trees

Vocalizations

Some of the vocalizations were recorded on a Uher model 4000 Report-L tape recorder with an AKG D 900 shotgun microphone. Frequency versus time plots were produced on a model 651A Kay Electric Company Vibralizer set for flat response and a 195 Hz narrow band width.

RESULTS AND DISCUSSION

Population Density

In the autumn of 1971, 27 squirrels controlled territories on the Bonanza Creek grid. This is a density of 1.23 squirrels per hectare (one squirrel per 0.78 ha). It is the greatest density yet recorded on the study area, as shown in Table 1. These are minimal estimates of total density since they represent only densities of territorial squirrels. The densities of nonterritorial, or vagrant squirrels are unknown. The location of each midden on the Bonanza Creek grid is shown in Figure 2.

Ten squirrels held territories on the Ballaine Road study area in the spring of 1971. Although many changes in territory ownership and boundaries occurred during the summer, the fall population stabilized at nine. This is a density of only 0.47 squirrels per hectare (one squirrel per 2.1 ha). However, only 29% of the study area contained suitable habitat for red squirrels. There was a density of 1.7 squirrels per hectare (one squirrel per 0.6 ha) of usable habitat. This supports Brink's (1964) observations that mixed stands of white and black spruce support squirrel densities similar to those in pure stands of white spruce. Figure 3 shows the location of each midden on the Ballaine Road study area in 1971.

Table 1. Estimated population size and density of the Bonanza Creek study area based on the number of active middens.

Season and Year	Estimated Population Size	Estimated Population Density	
		Squirrels Per Hectare	Hectares Per Squirrel
Fall 1964	10[a]	0.47	2.1
Fall 1965	4[a]	0.19	5.25
Fall 1966	no data	----	----
Fall 1967	23[b]	1.10	0.09
Fall 1968	18[c]	0.86	1.2
Fall 1969	no data	----	----
Fall 1970	no data	----	----
Fall 1971	27	1.28	0.75

[a]Derived from M. C. Smith (1967)

[b]Streubel (1968)

[c]Krasnowski (1969)

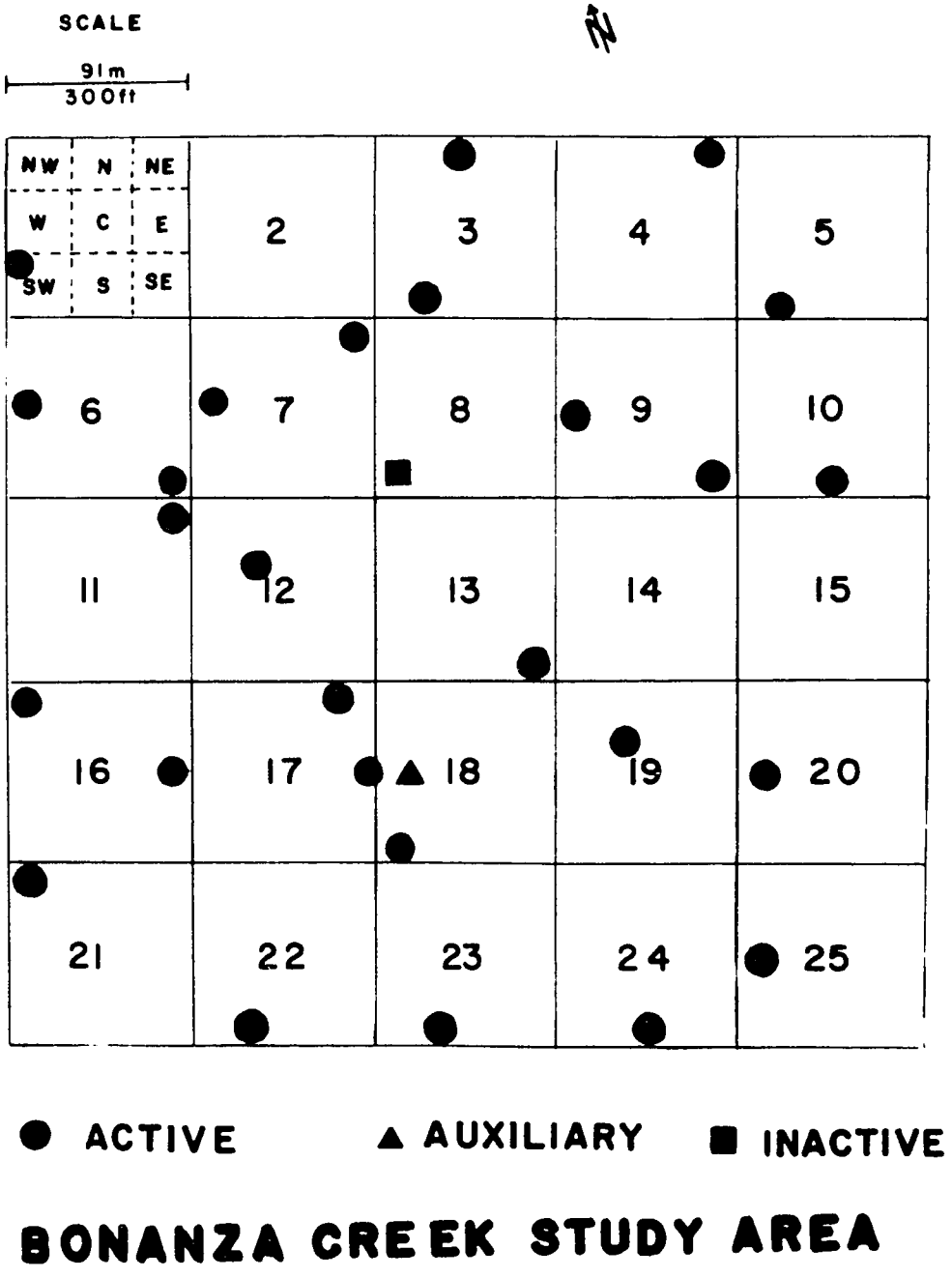

Figure 2. Location and status of each midden on the ... Creek study area, autumn of 1971.

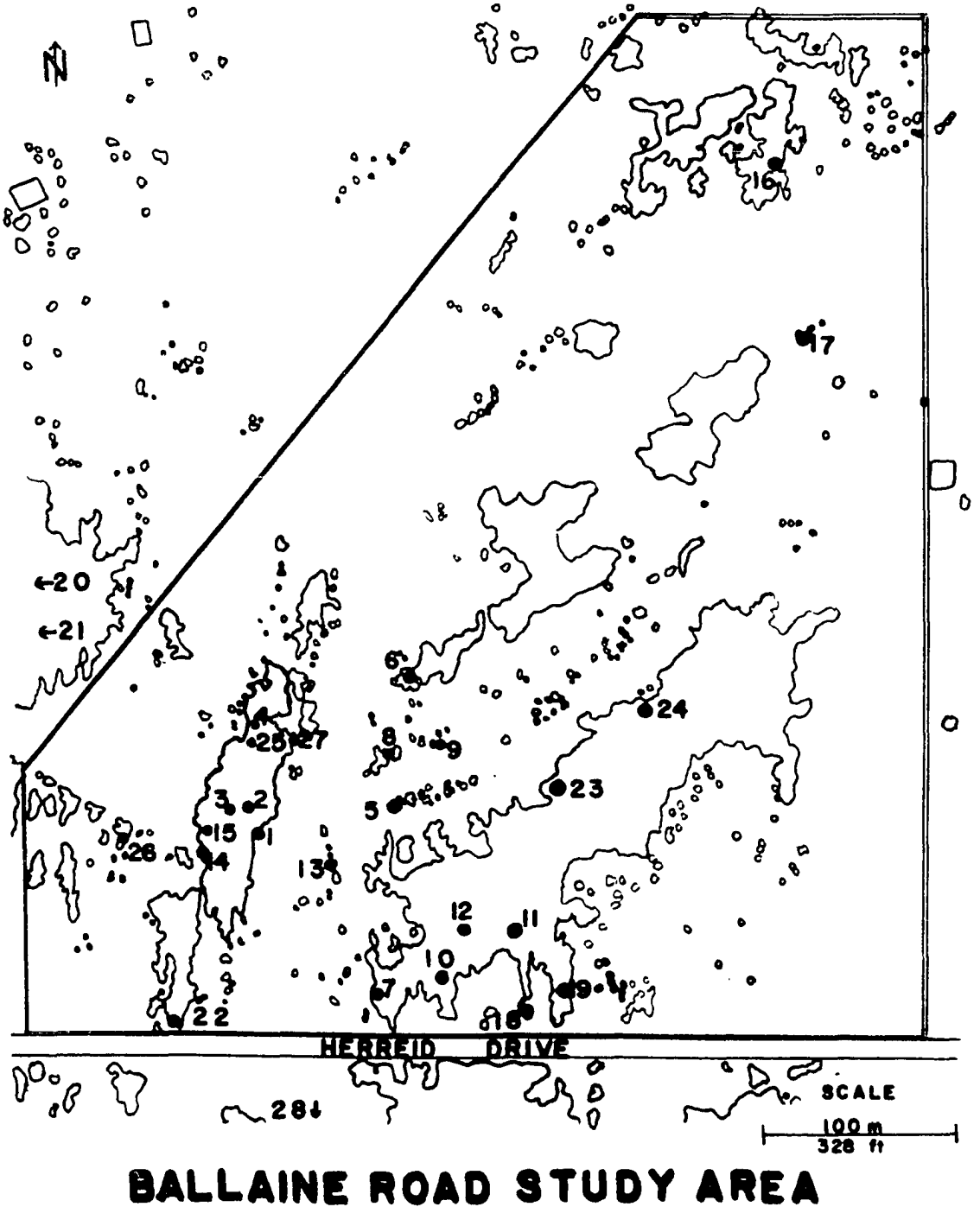

Figure 3. Location of each midden on the Ballaine Road study area, 1971. The 19-ha area of intensive study is enclosed by the double line. Only a few observations were made at middens 20, 21, and 28.

Food Habits

Utilization of Spruce Seed by Red Squirrels

There were great qualitative and quantitative differences in food supply on the two study areas. Therefore, a brief discussion of previous work on food habits and preferences of the red squirrel is included here.

Spruce seed is the major source of food for the red squirrel in interior Alaska. Fungi, fruits, and aspen buds are supplemental to the staple diet when available. Squirrels consume spruce buds when other food supplies dwindle (M. C. Smith, 1968).

Brink (1966) investigated squirrel utilization of the two spruce species available in the Fairbanks area. He reported a marked preference for white spruce seed over black spruce seed by captive squirrels. Squirrels steadily lost weight when experimentally fed black spruce cones only, but maintained weight on a white spruce diet. Calorimetric analysis showed about 9% more calories per gram in white spruce seed. Brink felt that this small difference in calorimetric value could not account for the different responses to black and white spruce diets. He concluded that black spruce seed lacked some essential nutrient supplied by white spruce.

There are problems to be overcome in keeping white spruce cones intact and sound over the course of a year.

In interior Alaska, most white spruce cones open in August (Zasada, 1971). If cones are collected before ripening, conifer seeds spoil easily (Finley, 1969). Seed dispersal begins in late August or early September, and 75-90% of the seeds are shed within three or four months (Zasada, 1971). Therefore, squirrels must complete the harvest within a very limited time period. Once collected, white spruce cones must be protected from drying and excessive heat which causes spoilage (Finley, 1969). The cache or midden meets these demands. With several years of use, a loose spongy mixture of earth and cone bracts accumulates at the midden site. This medium is easily excavated for burial and retrieval of cones, and at the same time provides a cool, moist environment for storage in the summer.

Black spruce cones constitute a more dependable food supply. Semiserotinous black spruce cones may be stored on top of the ground, for they do not open when exposed to dry air during the summer months. Cones representing several seasons of production are often retained on black spruce trees; LeBarron (1948) in Minnesota found cones four years old containing 2% viable seed. Some sound seed was available in cones as old as 15 years. This phenomenon tends to buffer the effects of occasional cone crop failures upon a red squirrel population.

The white spruce stand is considered to be the superior habitat for the red squirrel in interior Alaska. It is capable of supporting dense populations following good cone crop years, but it is also subject to periods of more severe famine than the marginal black spruce habitat. Following a failure of the white spruce cone crop, squirrels badly deplete excess stored supplies. Two consecutive years of failure can result in drastic reduction of red squirrel densities (M. C. Smith, 1967). There are no comparative data on fluctuations of red squirrel densities in a black spruce forest. However, one would expect densities to be more stable on a long term basis in black spruce.

Bonanza Creek Experimental Forest

In the autumn of 1970, white spruce stands produced a bumper seed crop, with a cone crop rating of 10 (Zasada and Viereck, 1970). In June 1971, the ground on the Bonanza Creek study area was littered with cones that squirrels had cut the previous fall but failed to cache. In late summer, 1971, prior to the cone harvest, most of the middens still contained cones from the 1970 crop. The relative amounts of cones in each midden were ranked as described in the section on methods. One midden was excluded due to insufficient data on food levels. Of 28

middens, 11 were ranked as high, five as high-medium, three as medium, seven as low, and two as very low (see Fig. 4). Of the squirrels controlling these middens in the fall, 19 were identified by age and 21 by sex. The relationship of age and sex of the squirrels to the food supply in the middens is shown in Fig. 5 and Fig. 6. From these data, it appears that adults disproportionately control middens with higher preharvest food supplies.

The number of active middens on the Bonanza Creek grid has been used as a census technique for five different years. Counts were made in 1964 and 1965 (M. C. Smith), 1967 (Streubel, 1968), 1968 (Krasnowski, 1969), and in 1971 during the course of this study. The relative preharvest food supply on each midden is positively correlated with the number of years the midden has been reported as active. In all middens examined, the degree of decomposition of cones indicated that only a very low percentage was harvested prior to the fall of 1970. The relationship is shown in Table 2.

The cone crop rating in the fall of 1971 was one, signifying a complete cone crop failure. The presence of ripe cones on the trees does not appear to be a necessary stimulus for caching behavior. The squirrels at Bonanza Creek actively collected cones from the ground even though cones were absent from the trees.

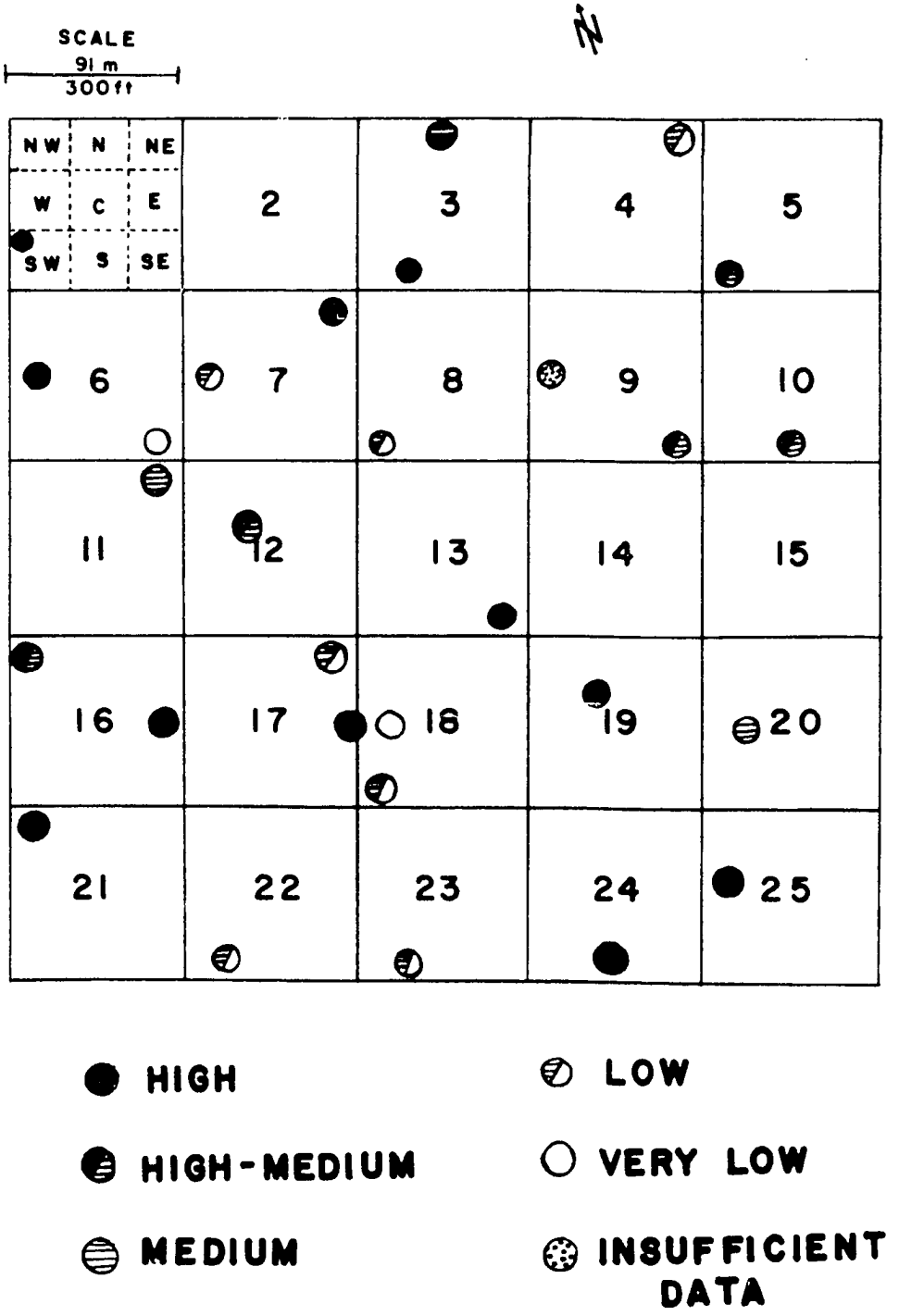

Figure 4. Relative amounts of cover remaining at each station on the Donnan Creek study area, late summer, 1971.

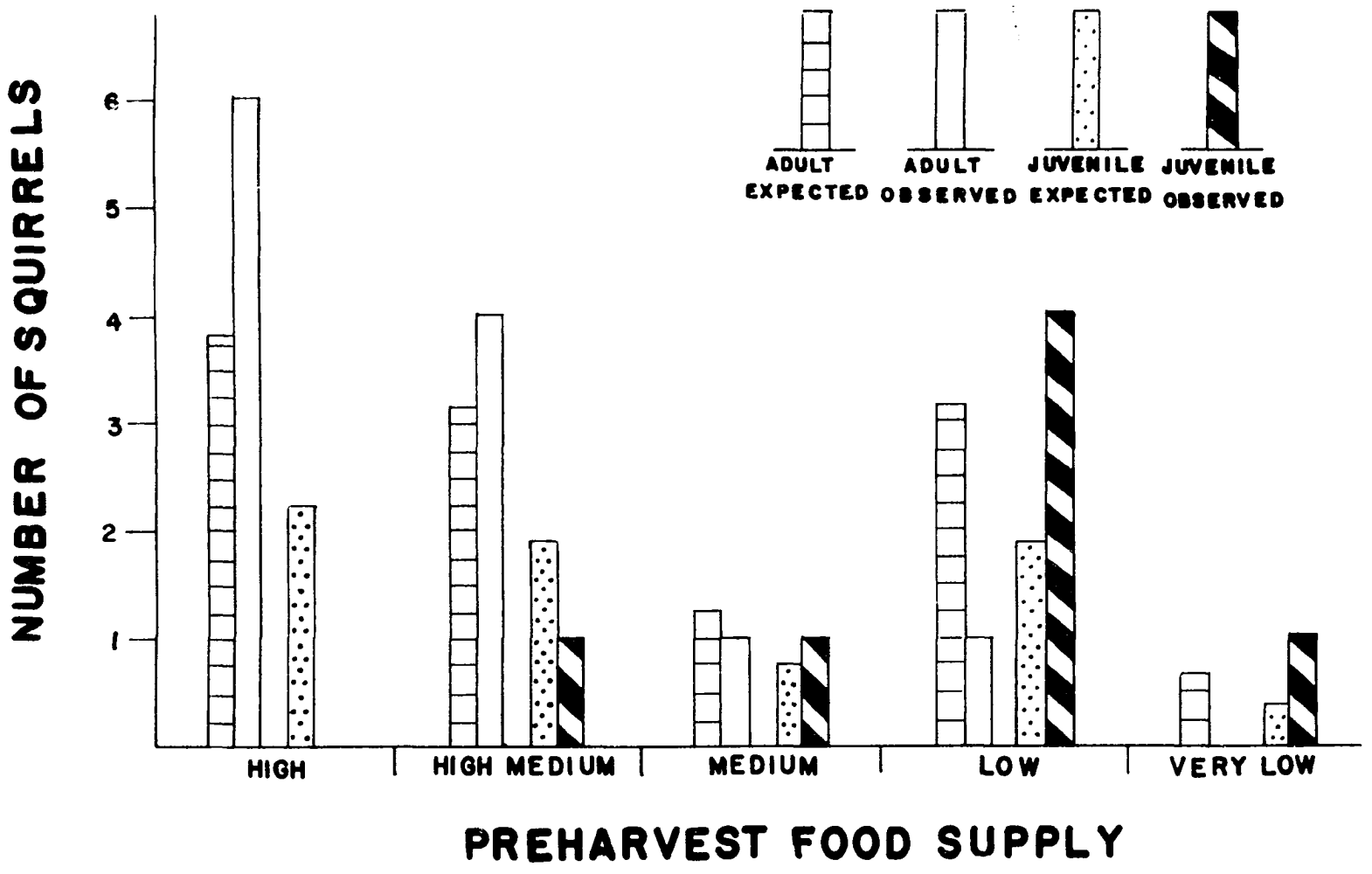

Figure 5. Preharvest food supplies on the Sonoma Creek middens in relation to the ages of the squirrels controlling them.

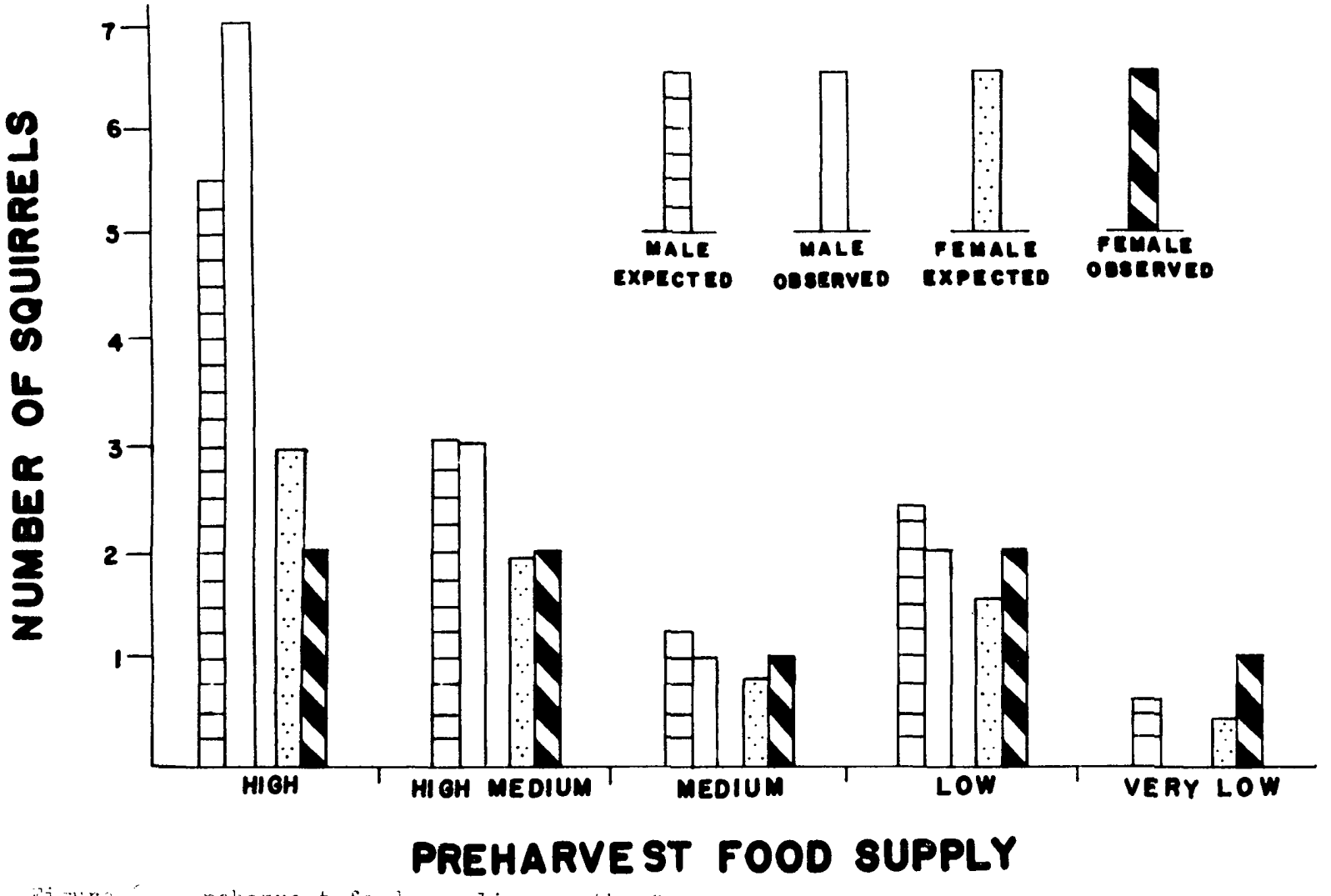

Figure 7. Preharvest food supplies on the Bonanza Creek middens in relation to the sex of the squirrels controlling them.

Table 2. Relationship of preharvest food supply in the midden, late summer, 1971, to number of years the midden has been reported as active. The numbers within the matrix represent the number of middens. (Data from 1964, 1965, 1967, 1968, and 1971.)

NUMBER OF YEARS THE MIDDEN WAS REPORTED ACTIVE

PREHARVEST FOOD SUPPLY IN MIDDEN, 1971	0	1	2	3	4	5
HIGH			1	3	3	1
HIGH-MEDIUM				2	4	1
MEDIUM				3		
LOW		3	2	1		
VERY LOW	2		1			

During the last two weeks of August, 1971, squirrels began to gather cones. Cone caching activity became intense in September. There were four possible sources of the sound cones collected by squirrels at Bonanza Creek. These were (a) cones cut in the autumn of 1970 which fell under logs or in moist depressions and were not retrieved at that time, (b) cones brought from auxiliary middens or small cone deposits buried near cutting trees, (c) cones raided from neighboring middens, and (d) cones excavated from the midden itself for inventory purposes. Except for two obvious cases from source d, it was assumed that all the cones piled on the middens were transported there from some other area. In several instances, squirrels were observed ranging from the midden, returning with a cone, and depositing it on the pile.

Only 5 of the 50 cones which I collected from the ground in early August contained filled seed. All of the freshly-cached cones taken from the middens in November contained some filled seed. The percentage of sound seed in the productive zone of the cones that contained filled seed was 61% for the ground cones and 66% for the newly-cached cones. If cones from the ground were a major source of the harvest, the squirrels were very selective in choosing cones for caching.

In only two cases were freshly cut cones observed in the piles. The squirrel at midden 9SE, an adult, piled about 150 freshly cut cones on her midden. These were old cones which had been clinging to the trees. The seeds had already been shed. The squirrel at midden 17E, age unknown, was observed cutting a branchlet of five cones on August 13. Three of these were open and the other two were empty of seeds. On September 3, the ground around midden 17E was littered with branchlets. Strangely, the squirrel had removed most of the cones from the branchlets and carried them separately to the pile. The cones from this pile were all empty. Cones from other piles on the midden were not freshly cut and contained sound seed.

An adult male at midden 7NE was observed carrying cones from a hole on one side of the midden to a burrow on the other side. Before depositing each cone, he stripped a few of the basal bracts, apparently checking the soundness of the seeds. I believe these cones were cached in the midden during the previous autumn.

In most cases, cones were not buried immediately, but instead were stored temporarily in piles on top of the midden. By September, squirrels were beginning to move cones into small depressions dug in the middens.

Caching and burial of cones continued until the latter half of October when the snow began to build up.

Even with 1 or 2 inches of snow on the ground, squirrels were actively cleaning out burrows and rearranging cones.

A rough minimum estimate of the amounts of cones cached at each midden is shown in Figure 7. Of 27 territorial squirrels on the grid, five squirrels gathered 35-70 liters, five gathered 15-20 liters, two gathered 500-1,000 cones, six gathered fewer than 200 cones, and at five middens there was no evidence of any caching activity. Four of the middens were not examined sufficiently to determine the amounts of cones cached. There does seem to be a correlation between age of the squirrel and the amount of cone caching activity. Juveniles made up a disproportionate number of the squirrels which cached no cones as shown in Fig. 8. There are no clear sexual differences in cone caching activity (See Fig. 9).

Ballaine Road

In the autumn of 1970, both white spruce and black spruce cones were available for caching on the Ballaine Road study area. The absence of black spruce bracts on the middens and at feeding stations indicated that only white spruce seeds were consumed during the late winter and spring. When the snow melted in early May, 1971, black spruce cones were found cached at only two middens, 14 and 16. The white spruce cones at both middens were plentiful and there was no evidence that the black spruce

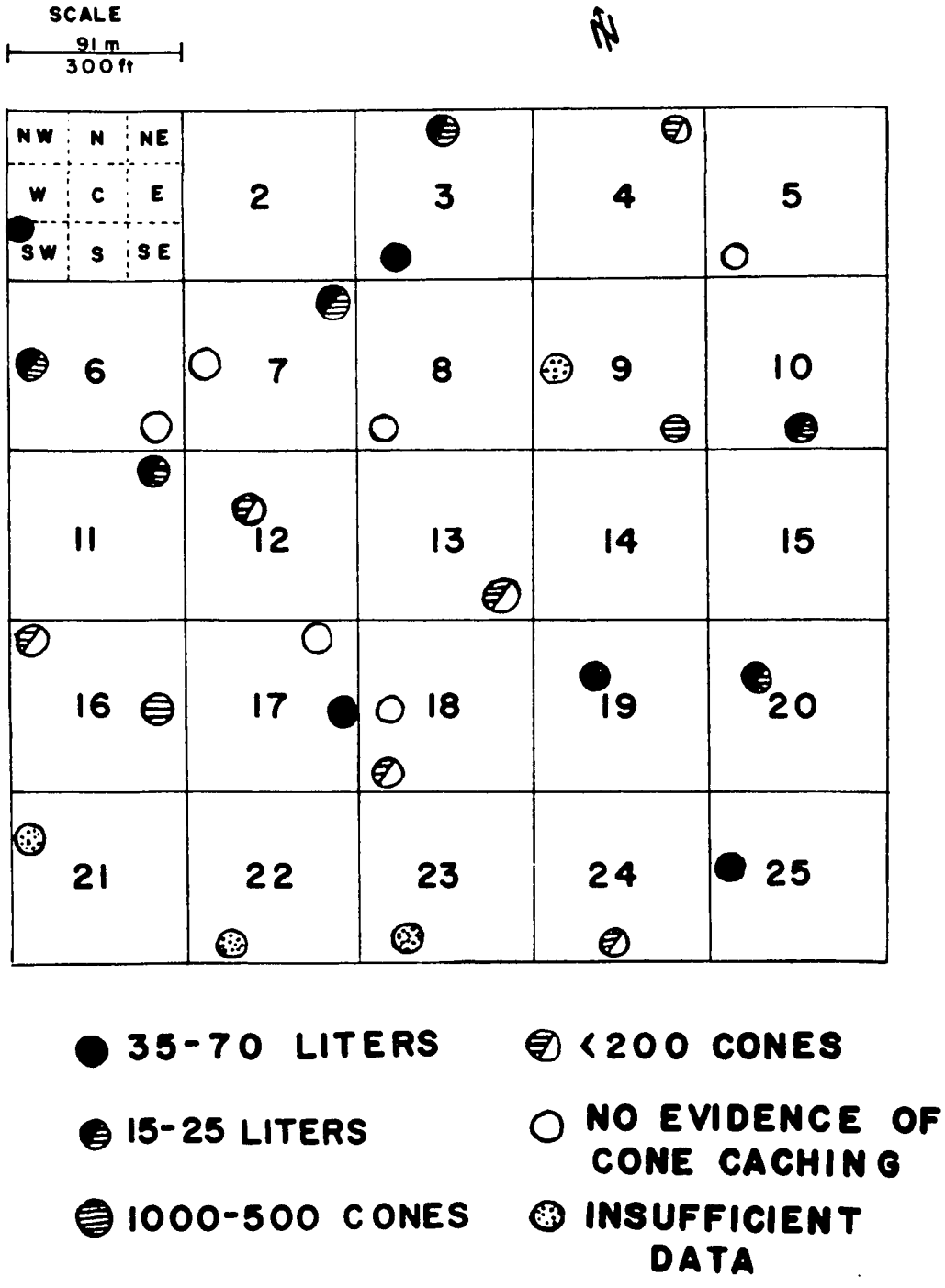

Figure 7. Estimate of amounts of cones cached at each midden in the fall of 1971 at Bonanza Creek.

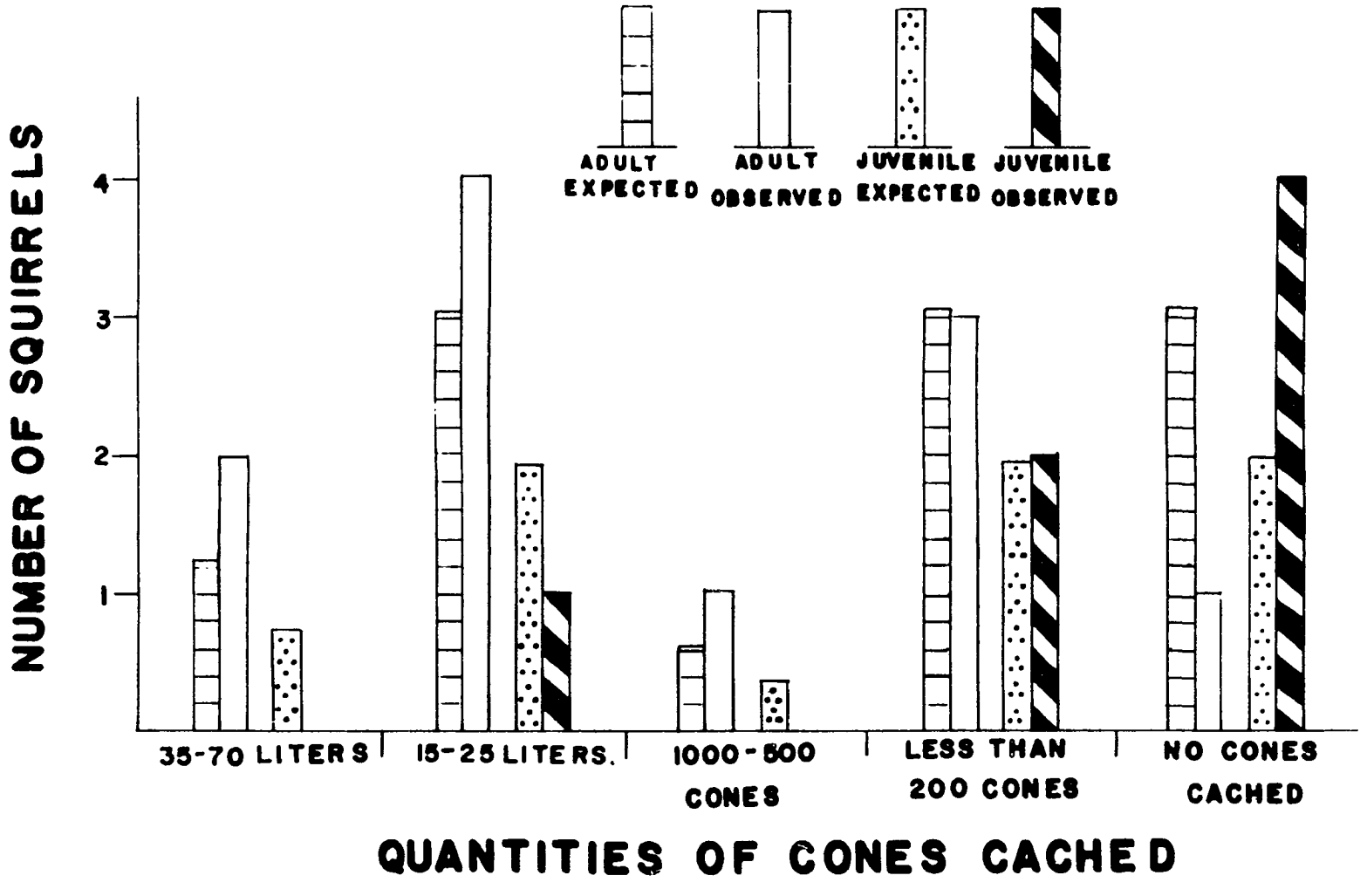

Figure 6. Age versus quantities of cones cached in 1971 at Sonmans Creek.

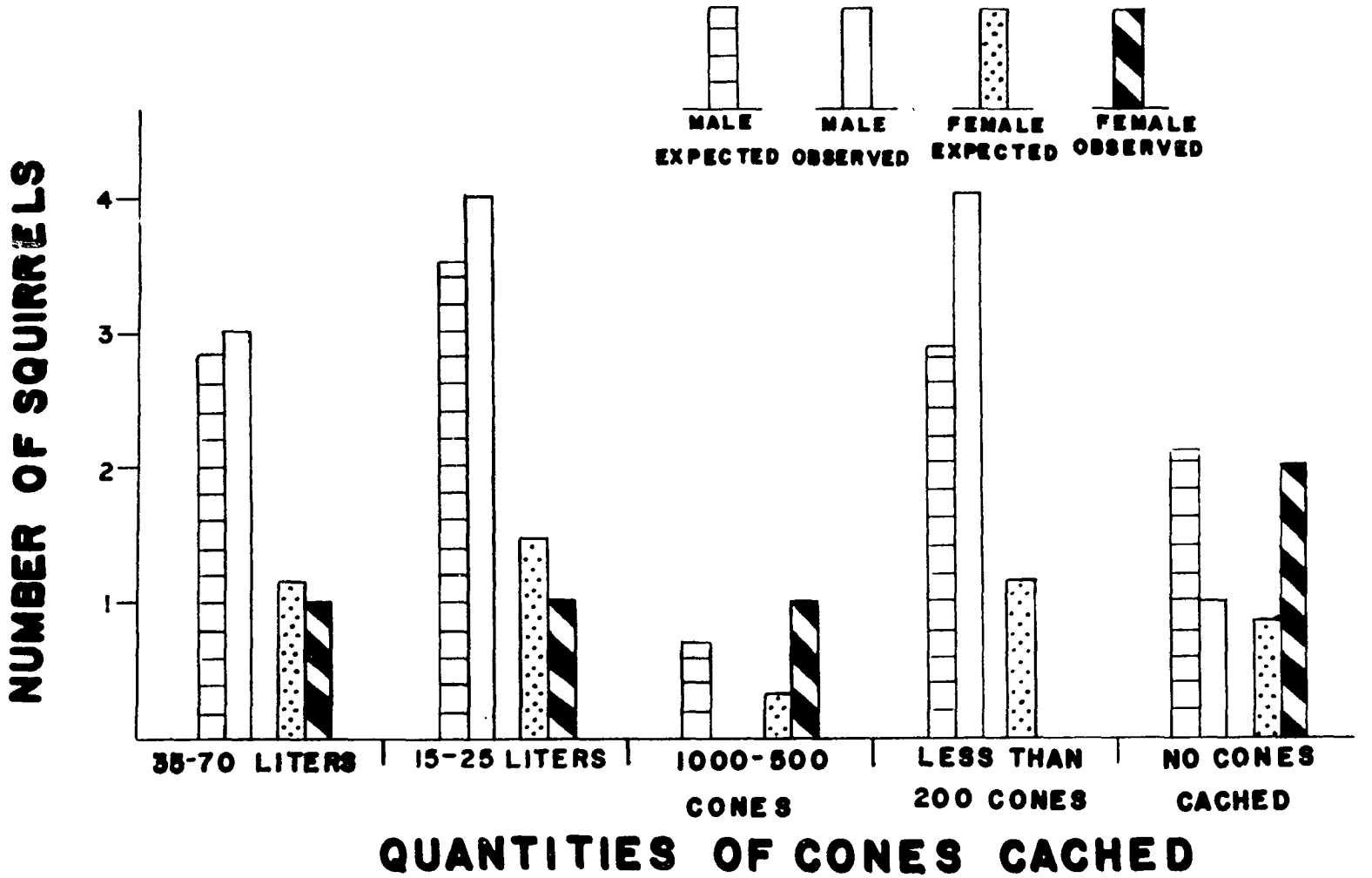

Figure 3. ... versus quantities of cones cached in 1971 at Bonanza Creek.

cones were being consumed. The black spruce cones were simply heaped in piles on the ground. In contrast, the white spruce cones were all buried or packed tightly into moist depressions.

Each squirrel's territory contained at least one large midden, and often two or more auxiliary middens. Even the major middens at Ballaine Road were considerably smaller than those at Bonanza Creek. Middens were located in isolated groves of productive white spruce trees. Caches were often situated at the base of a single large white spruce. A great many cones were cached in small pockets of 10 to 20 scattered around the forest floor, rather than being consolidated into discrete middens. In terms of time and energy during the harvest, it was probably advantageous to cache cones at several small middens. Caching all cones at one central midden would require numerous trips over the open areas between sheltering groves of trees. One would expect this system of cone caching to render defense of territory and food supply more difficult. On the other hand, if a portion of the territory were lost to a rival squirrel, the entire food supply would not be forfeited. During the cold periods in January and February, the squirrels rarely strayed more than a few feet from the major midden. With warmer temperatures in March and April, use of auxiliary middens increased. As the summer progressed,

the auxiliary middens became rapidly depleted. By September, very few cones were left, even at the major middens. The black spruce cones at middens 14 and 16 were consumed during July and August, as the white spruce cone supply became exhausted.

In the autumn of 1971, only black spruce cones were available for cutting. The caching habits of four juveniles and three adults were studied intensively at this time.

Juvenile male 42 (Tag numbers have been abbreviated in the text. See Appendix A for complete ear tag numbers.) at midden 4-BR was observed cutting black spruce cones on July 15. It is doubtful that the seeds were ripe at this early date. Despite his early initiative, this squirrel cut sporadically for the rest of the season. He managed to amass only about 20 liters of cones. It is interesting to note that while he originally cut cones singly, he later learned to cut branchlets, thereby facilitating transport to the midden. The three adult males on the study area cut all their cones on branchlets, even at the beginning of the season. As mentioned previously, the semiserotinous black spruce cones need not be buried to prevent drying. This juvenile male buried his black spruce cones, an unnecessary expenditure of energy. In contrast, the adult squirrels simply piled the cones they cut on top of the ground. This suggests that knowledge that semiserotinous cones can be stored on the surface is not innate, but

learned. Finley (1969) found that red squirrels in the Rocky Mountains also cached serotinous lodgepole pine cones on the surface of the midden. Neighboring juvenile male, squirrel 40 at midden 25-BR, was never observed cutting cones for storage, although more time was devoted to observation of this squirrel than any other. He established his territory about a sack of dog food and defended it in exactly the same manner as those squirrels controlling more traditional middens. His internal motivation to cache cones was strong, but he preferred raiding midden 4 to cutting his own cones. He was observed cutting black spruce cones from a tree on September 3, but these he consumed while still in the tree. He was observed raiding midden 4 on three occasions, making several trips for cones and dried mushrooms. Although black spruce cones were buried along with white spruce cones on midden 4, squirrel 40 searched out the white spruce to carry back to his cache. He was able through his raiding activities to gather an adequate supply of cones to survive the winter. He also controlled a section of the grove in which numerous deposits of cones had been cached by the previous occupant of the territory. Midden 25 was still active at the end of the study period in December, 1971.

Juvenile male squirrel 14 at midden 14-BR cached cones at a rate equal to or less than his consumption, so as winter

approached, his stores were very low. In October, he deserted his midden and the study area. In March, 1972, he returned to the study area and established himself at midden 25, two weeks after the removal of squirrel 40 from that midden. Midden 14 remained inactive through the winter and spring of 1972.

Juvenile female, squirrel 76 at midden 6-BR, cached fewer than 100 white spruce cones, starting on October 19, quite late in the season. The source of these cones was probably one of the small auxiliary middens surrounding midden 6. She deserted her midden in mid-winter, and was shot on April 23, 1972, at a bird feeder located about 0.5 km from the center of her territory.

The three adult males at Ballaine Road, in contrast to the juveniles, were active at cutting and caching black spruce cones. These were squirrels 17 at midden 18-BR, 12 at midden 16-BR, and 81 at midden 28-BR.

Midden 28-BR was atypical in that in the autumn of 1971 it was well stocked with white spruce cones cached during the previous year. In spite of an already adequate food supply, this squirrel cut and cached more black spruce cones than any other individual on the study area.

Each squirrel, whether adult or juvenile, concentrated all his caching activities on the major midden, neglecting the auxiliary middens. Thus, while the density of territorial

squirrels in the spring and fall of 1971 did not change greatly, there were 25 middens in use in the spring and only nine being used in the fall.

Vocalizations

Territorial Call

The territorial call (see Appendix B) was emitted during all three types of territorial defense as described in the following section on territorial behavior. The calls were identical in the three forms of defense except for duration, as observed by C. C. Smith (1968). Broadcast territorial calls, which served to announce the presence of the owner on the territory, were usually emitted with no apparent external stimulus. They were often accompanied by offensive threat calls, but rarely by tail lashing, which is reserved for boundary disputes and chases.

Occasionally, a territorial call was emitted immediately following the call of a neighboring squirrel. This probably occurs when a squirrel's internal motivation to call is already at a high level. The external stimulus of another call may then cause an immediate response. When the internal motivation is not near a peak, no response will be made to another call. Usually, there is no apparent response of any kind to the call of another squirrel (C. C. Smith, 1965).

Exceptions occurred when the call was close, for example when both individuals were near a mutual boundary. Exchanges of territorial calls often occurred in which 20 to 30 calls were emitted within the span of a few minutes.

If the squirrels were within sight of one another, the calls were extended in length. When chasing occurred during boundary disputes, territorial calls were emitted by the individual that was dominant at that point. Dominance shifted from one dispute to the next, or even during the course of a single dispute. When both squirrels emitted territorial calls, they were probably evenly matched in dominance. These calls were not just generally broadcast, but were stimulated by, and directed at another individual. They seemed to display ownership of a territory and willingness to defend it.

Finally, territorial calls were emitted by the owner while chasing an invading squirrel from the territory. This call was also used for interspecific interactions. C. C. Smith (1968) reported that the territorial call was recognized by the Douglas squirrel, Tamiasciurus douglasii. In the present study, it was observed that the territorial call was given in response to any animal the squirrel wished to drive from the territory. Squirrels were observed directing territorial calls at humans, gray jays, Perisoreus canadensis, a snowshoe hare, Lepus americanus, and a short-tailed weasel, Mustela erminea. The squirrels aggressively chased the other animals, with the exception of humans, from the midden areas. The weasel avoided the midden after he was chased, and on another occasion, was seen to hurry for

cover when the squirrel that had chased him emitted a territorial call close by. Interspecific chases differed from intraspecific chases only by the slightly lesser degree of intensity of the attack. Also, while squirrels were chased from any part of the territory other animals were only driven off when they trespassed on the midden itself.

Squirrels rarely emitted territorial calls while confined in traps. However, frequently the territorial call was emitted immediately after release; see the combined summary of data from both study areas shown in Table 3.

This information has practical application for future workers. One can be quite certain that if a territorial call is emitted immediately after release from a live trap, then the squirrel is on his own territory. Sources of error occur when territorial calls are emitted on a midden which is in a state of flux in regard to ownership. Also, very young juveniles begin to call before they have left the mother's territory (C. C. Smith, 1965). If no call is given on release, it is more difficult to determine the squirrel's status as territory owner or invader. In three cases, squirrels trapped while off their territories, ran immediately to their own middens and emitted the territorial call there.

C. C. Smith (1965) reported that all squirrels involved

Table 3. Summary of releases from live traps and emission of territorial calls.

	No. of releases in which territorial calls were given
101 captures on squirrel's own midden	70
7 captures probably on squirrel's own midden	4
19 captures not on squirrel's own midden	0
1 capture probably not on squirrel's own midden	0
16 captures on inactive middens (not controlled by any squirrel)	5
3 captures on boundary of squirrel's own territory	0
147 total captures	79

in breeding chases, including the female, may occasionally emit territorial calls. He felt that subordinate males called less frequently than the dominant male. They seemed to call only when very close to the female, or while attempting to approach her. In April, 1972, a single male was seen pursuing a female in the vicinity of middens 1-BR, 2-BR, and 3-BR. These middens were inactive and undefended at that time. The chase progressed to midden 25-BR, and finally up to the boundary which had been previously established by squirrels 40 and 42. (Squirrel 40 had been removed in early March.) Squirrel 42 approached from midden 4-BR, emitting territorial calls. The other male had been emitting only a soft buzzy note, the appeasing call. Four attempts were made by squirrel 42 to reach the female. Each time, he emitted the territorial call, but was driven off by his rival. Finally, the female left and ran toward midden 1-BR. She was followed by the untagged male, but male 42 remained at the boundary emitting a succession of territorial calls. At no time during the incident did either the female or the dominant male emit territorial calls. In another breeding chase observed in April, 1971, only the buzzy appeasing call was heard. Territorial calls were conspicuously absent.

The Alarm Call

See Appendix B for an example of the alarm call.

C. C. Smith (1965) stated that "the function of the call is to warn conspecific individuals of the presence of predators" and that "it seems basically altruistic". He argued that a necessary condition for the development of such calls is that closely related individuals must live within hearing distance of one another. He found that juvenile squirrels did in fact tend to establish territories near littermates, and often near one or both parents. Observations of territory establishment by juveniles during the present study support these findings. Thus, the necessary condition for kinship selection is present.

However, alarm calls were emitted in response to a much broader range of conditions than those discussed by C. C. Smith. Most of the alarm calls heard were in response to predators or potential predators. Humans fell into this category since they are probably regarded as predators until the squirrel has learned otherwise. At Ballaine Road, some of the squirrels had been in long term contact with humans, and would tolerate them at close quarters without emitting the alarm call. C. C. Smith (1968) assumed that a red squirrel increases his probability of being captured by a predator by emitting alarm calls, thus betraying his location to the predator. In my observations of squirrel-predator interactions, squirrels called from the safety of arboreal perches, where neither ground nor avian predators

could reach them. Squirrels calling from trees would be at a disadvantage only when confronted by tree-climbing predators, or humans with guns. Layne (1954) indicated that red squirrels subjected to shooting pressure soon learned to be quiet when humans were in the vicinity. Observations of vocalizations emitted during squirrel-marten interactions would be informative. I believe the assumption that red squirrels expose themselves to danger by emitting alarm calls is unwarrented, in most squirrel-predator interactions.

Alarm calls were also given under a variety of circumstances which did not involve predators. Alarm calls were commonly emitted during both boundary disputes and basically nonaggressive interactions. Alarm calls, as well as defensive threat calls were often emitted by the subordinate individual in boundary disputes. They were not emitted by the more dominant squirrel. Also, during observations made of juvenile sexual play along the territory boundary, alarm calls were emitted if the other participant became overly rough or aggressive. In a later discussion of interactions between trapped and free squirrels, an incident is described in which both squirrels were on neutral ground. The free squirrel appeared to desire engagement in aggressive interaction, but lacked the confidence of squirrels on their own territories. He was not able to follow through on his

charges at the trap, and fled when he reached it rather than fighting. Following one of these truncated attacks, the free squirrel climbed a nearby tree, and began to emit the alarm call. It was interpreted as a response to fear and frustration due to his inability to cope with the situation.

Red squirrels also responded to surprise by emitting alarm calls, even when no real element of danger was involved. This initial response was as expected, because a surprise may often be a predator. However, the alarm call was emitted long after the squirrel had been able to determine that there was no danger.

Alarm calls were emitted during any kind of frustrating situation. A squirrel was observed attempting to cache a large bracket fungus on a tree branch near his midden. The fungus was carried up the tree three times, but each time it was deposited on the branch it fell off. The squirrel began emitting alarm calls the first time it fell, and the calls became progressively louder with each subsequent failure. Finally, the fungus was abandoned where it fell. On another occasion, an adult female was observed sniffing a baited trap while emitting alarm calls. She had never been trap-shy before, but on the previous day, had gone into shock during handling. Fear of the trap, and frustration because she wanted the bait probably both served as stimuli for

the alarm calls.

Fear, frustration, and surprise are all stress producing factors. Alarm calls were produced when one, two, or all of these elements were present. Thus, perhaps a broader interpretation of alarm call function is more suitable than that proposed by C. C. Smith (1965). As an alternative explanation, the alarm call has a tension relieving function, as proposed by Hazard (1960). He proposed the same function for displacement drumming of the legs which often accompanies alarm calls. He also felt that the drumming might cause a response of some kind by the object which stimulated the calls. This response would then help the squirrel to identify the object as dangerous or harmless. Warning nearby relatives of danger could be incidental to the production of alarm calls, but it is questionable whether this has been the major driving force in its evolution.

Aggressive Calls

C. C. Smith (1968) described two types of aggressive calls emitted by red squirrels. These could not be differentiated in the field, but only by analysis of sonograms. During the present study, two aggressive calls were readily distinguished in the field. See Fig. 10 and Appendix B.

The first call, which has been named the offensive threat

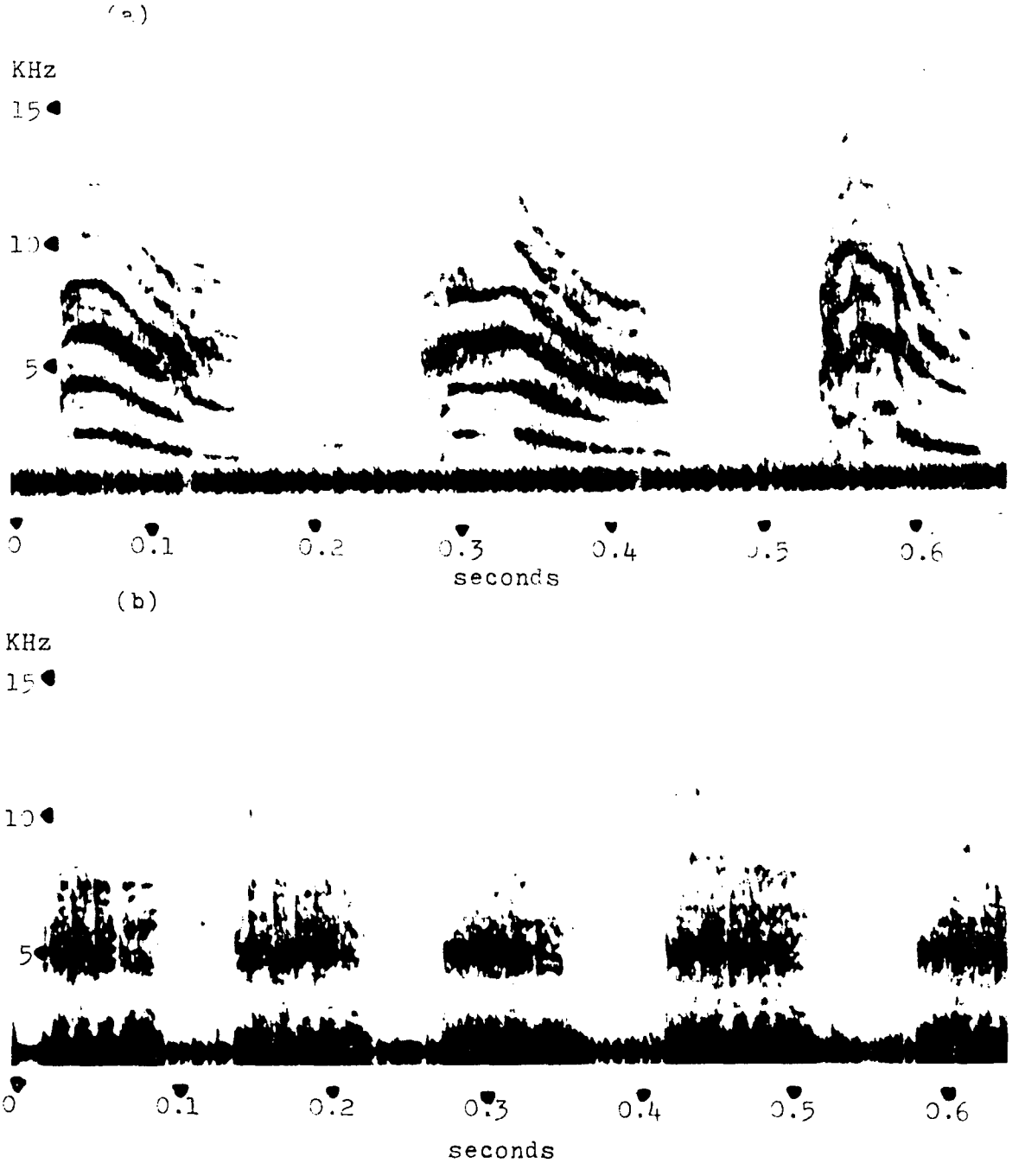

Figure 10. Notes from aggressive calls; (a) offensive threat call; (b) defensive threat call.

call, corresponds in function to the loud-agressive call referred to by C. C. Smith (1968). It often accompanied the territorial call during chases and was emitted by the dominant squirrel during boundary disputes. During interactions between trapped and untrapped squirrels, it was emitted by the owner of the territory, if he was the free squirrel. In function, the offensive threat call seems close to that of the territorial call. The distinction between the functions of the two calls is still unclear.

The second type of aggressive call recognized has been named the defensive threat call. This is the quiet-aggressive call described by C. C. Smith (1965). During the present study, it was emitted under a variety of circumstances, but all seemed to indicate aggressive intent by a subordinate animal, or by an animal which was trying desperately to defend itself. During boundary disputes, the emission of defensive threat calls was the first sign that one of the squirrels was losing confidence. Even though a squirrel desires to flee to the safety of the midden, he presumably feels forced to stay and defend the boundary. Otherwise, a portion of the territory may be lost. Defensive threat calls were emitted by an invader in a live trap, while fighting with the owner of the territory. When both the owner and the invader were in traps, placed side by side, both emitted the defensive threat call. As soon as the

owner was released, his vocalizations changed to offensive threat and territorial calls. The defensive threat call was sometimes emitted as a human approached a live-trapped squirrel. This was also reported by C. C. Smith (1965). Finally, the defensive threat call was emitted during mounting and play activity between two juvenile males when one became too rough or persistent. It was emitted only by the individual being mounted, as he attempted to pull away. C. C. Smith (1965) described the call as being given by females during copulation, while attempting to escape from the male.

Appeasing Calls

A soft buzz is frequently emitted by adult male squirrels during breeding chases, and was for this reason referred to as the mating call by earlier workers (Layne, 1954; Hazard, 1960). C. C. Smith (1965) found that it is also used by females and juveniles outside of the breeding season. Its function appears to be a communication of nonaggressive intent toward other squirrels. Therefore, C. C. Smith has used the term appeasing call, which better describes the broader function of this vocalization. During the course of the present study, this buzzy appeasing call was heard only during breeding chases. It was emitted only by the males.

Another call was emitted by juveniles which also seemed to serve an appeasing function. Adult female squirrel Ol

moved her litter into the vicinity of midden 8SW-BC and remained there for several days while the juveniles established their territories at nearby middens. On July 23, 1971, one of the juveniles was trapped at 8SW. It escaped during handling and was immediately chased into a tree by adult male 73. The juvenile began emitting calls which sounded like the whimpering of a puppy. The juvenile ran down the tree and up another, still whimpering. The adult male did not resume the chase, but left the area. As soon as the adult was gone, the juvenile ceased whimpering and gave a series of territorial calls in rapid succession. On July 27, 1971, one of the juveniles started down from a tree near 8SW just as his mother was being released from the trap. Adult male 73 approached from the North and chased the juvenile up and around a tree just south of the trap. Upon reaching the ground again, the juvenile began whimpering. The adult male remained in the tree and gave a territorial call. The juvenile moved freely about on the midden for 10 minutes, still whimpering, then finally moved off to the South, out of sight. The adult female remained a short distance away, but did not attempt to enter into the interaction, nor did she appear to be disturbed by it. C. C. Smith (1965) observed that the buzzy appeasing call was emitted by juveniles while trespassing on an adult squirrel's territory. The whimper appeasing call thus appears to have a

similar function. One significant difference in their functions may be that the whimper is used when the juvenile is on home ground. The aggressive adult male was not on his own territory. The whimper may be used by very young juveniles, before they have left the mother, while the buzz is used by older juveniles.

A third type of appeasing call was emitted by two juvenile male littermates while involved in occasional play activities along the border of their adjacent territories. Very low amplitude, high pitched squeaks were emitted by both squirrels during these interactions. The squeaks were used particularly when one squirrel approached the other. The call appeared to signal not only lack of aggressive intent but also desire and willingness to participate in very close physical contact.

Territorial Behavior

Territorial Marking and Defense

Kemp and Keith (1970) distinguished two types of territories. In deciduous areas, squirrels were free-ranging in summer but defended transient winter food caches. Prime territories, located in coniferous habitat were defended continuously, both summer and winter. Since no large, deciduous stands were examined during this study, and the territories observed were defended year round, the following discussion of territorial behavior deals strictly with the so-called "prime territories".

The territorial call was broadcast at irregular intervals as an announcement that the owner was present on the territory. This call was usually emitted with no apparent external stimulus. The effectiveness of these broadcast calls as deterrents of invasion was demonstrated on three occasions. In each case, the invading squirrel was observed raiding cones, when a territorial call was heard from another portion of the territory. The territorial owner was not in sight, but the call alone was enough to cause the invader to cease raiding activities and return to his own territory. It is believed that the owners of the territories were unaware that the invasions had occurred.

Chases occurred when an owner discovered another squirrel in his territory. Discovery of the invader occurred in only

seven of the 29 incidents of trespass observed.

Twice, squirrel 42 was observed raiding midden 25-BR, when the owner, squirrel 40, approached. Both were juvenile males. The chase began immediately, with the owner emitting territorial calls and offensive threat calls. The invader did not attempt to fight but fled directly to his own midden, 4-BR. In both pursuits, the owner stopped chasing and emitted the territorial call when he reached the boundary. His calls were answered by squirrel 42 from midden 4.

Three other chases were observed already in progress. One chase involved two adult males. One involved two juvenile males. The third chase was between two untagged adults of undetermined sex. The chases all followed the same pattern. They were high speed, with the owner calling frequently, sometimes pausing to call and lash the tail from side to side. Both territorial and offensive threat calls were emitted. In all three instances the invader ran silently until he was out of sight. In two chases the owner stopped at the boundary, and called after the disappearing invader. In the chase involving the untagged squirrels, the position of the boundary was unknown, but the owner did cease the chase before reaching the invader's midden.

In two interactions, the invader was not so easily repelled. On July 28, 1971, juvenile male 42 was chased around his own midden, 4-BR, by a large untagged squirrel. At this time, the juvenile weighed under 200 g, while the

estimated weight of the untagged squirrel was 240 g or more. The larger squirrel was silent during the entire interaction. The territory owner alternately emitted territorial and alarm calls, even as he was being chased. As the chase became more intense, he began to emit defensive threat calls also. After five minutes of chasing, the invader suddenly broke off and left the midden. Squirrel 42 remained on the midden and emitted several territorial calls in rapid succession. On November 1, 1971, squirrel 42 and squirrel 40 were heard calling from the boundary between their territories. Upon investigation, a large untagged squirrel, probably adult, was seen to be also in the boundary area. Squirrel 42 was emitting defensive threat calls, and squirrel 40 emitted territorial calls. The invader quickly left the area at my approach. He was not followed by either of the territorial squirrels.

Another manifestation of territorial behavior observed was the boundary dispute. High intensity boundary disputes involving the same two squirrels, 42 from midden 4-BR and 40 from midden 25-BR, are described here. They are considered to be typical since the behavior was similar to disputes between other squirrels.

All four disputes took place in a small area along the boundary between their middens, 8 m from the center of midden 4-BR, and 16 m from midden 25-BR. At this point,

the boundary was a narrow corridor approximately 3 m wide. The rest of the boundary was considerably wider, with both squirrels frequenting a number of trees which neither seemed to actively defend. Each squirrel had a favorite perch from which he often called when not disputing. These two perches, plus a balsam poplar tree, Populus balsamifera, on neutral ground served as the major sites for both aggressive and nonaggressive interactions.

On July 29, 1971, squirrel 42 was at his perch emitting territorial calls. Squirrel 40 was on the ground in the neutral strip emitting territorial and alarm calls. After three minutes of calling, squirrel 42 chased squirrel 40 to within 3 m of midden 25, before returning to midden 4. A few more territorial and offensive threat calls were emitted before the dispute dissolved.

On October 14, 1971, squirrel 40 was at his perch emitting territorial calls. Squirrel 42 gave defensive threat calls and territorial calls from his perch. Squirrel 40 began chasing the other to midden 4. Territorial calls were given simultaneously by squirrel 42 on midden 4, and squirrel 40, only 5 m away. Then squirrel 40 ran back to his own midden and gave the territorial call there. Squirrel 42 did not chase but climbed the neutral balsam poplar tree and returned the call.

On December 6, 1971, the third dispute was observed.

Squirrel 42 was emitting defensive threat and territorial calls from his perch. Squirrel 40 was on the neutral tree emitting territorial calls. The latter climbed down and approached midden 4. He was chased by squirrel 42, and a brief fight occurred. The squirrels displayed the vertical "boxing" posture, as described in the next section. Squirrel 40 ran back to midden 25, while squirrel 42 called from his perch at the boundary.

The fourth dispute was observed on December 16, 1971. Both squirrels were emitting territorial and offensive threat calls. When I reached the area, squirrel 42 was positioned on the neutral tree. He began emitting alarm calls. Squirrel 40 was on the other squirrel's perch, emitting territorial calls. Squirrel 42 fled to midden 4, and squirrel 40 ran after him. At midden 4, the chase reversed, with squirrel 40 emitting defensive threat calls all the way to midden 25. He gave the territorial call upon reaching the midden. Squirrel 42 answered from his perch at the boundary.

In all high intensity boundary disputes, the squirrels were highly excited. They hopped rapidly about their perches, making themselves highly visible to the rival. They paused only while emitting territorial and offensive threat calls, but even then, violent tail lashing maintained the high visibility. Territorial and offensive threat calls were usually emitted by both at the start of the dispute. As the interaction progressed, one squirrel would begin to

show signs of uneasiness or subordinance by emitting alarm and/or defensive threat calls. The dominant squirrel would then begin the chase, or at least follow after the subordinate had retreated. As shown in the previous interactions, dominance shifted as the chase neared the subordinate squirrel's midden.

Low intensity disputes were observed on several occasions. Two squirrels typically would exchange several territorial and offensive threat calls without being in visual contact. Excitement was much lower than in high intensity disputes. Calls were not accompanied by tail lashing. Usually, the squirrels continued their normal activities, feeding, grooming, etc., during the low intensity disputes. This differed from the high intensity dispute where attention was directed completely at the other squirrel.

Interactions Involving Trapped Squirrels

Only disputes involving free squirrels were discussed in the previous section. Interactions involving trapped squirrels are discussed separately, since confinement of one individual in a trap may in some way alter the dominance of the squirrels. Six of the interactions occurred when squirrels entered traps off of their own territories. In four of the interactions, trapped squirrels were placed experimentally upon a neighboring territory. In this way, the entire interaction could be observed.

On July 25, 1971, squirrel 40 was trapped at his midden, 25-BR. He was placed in a cage constructed of chicken wire with dimensions 87 x 116 x 174 cm. The larger cage was used since it was feared that the smaller live trap would restrict free movement. This fear proved to be unnecessary, however, since the interaction was identical to similar situations in which squirrels were confined in live traps. Cage and squirrel were moved to midden 4-BR, controlled by squirrel 42. Both squirrels were juvenile males, and they had been established at their respective middens for over a month. At 1010, the cage was placed on midden 4. Squirrel 42 approached the cage immediately, even before I moved away. At 1011, he began to chase the captive around the cage, pausing every few seconds to lash his tail from side to side and emit extended territorial calls. Offensive threat calls were given before and after territorial calls. During these pauses, squirrel 40 chewed frantically at the cage, trying to escape. As the free squirrel resumed the chase, the captive ran around the cage, avoiding contact. At 1012, the first fight occurred, lasting only a few seconds. Squirrel 40 emitted the defensive threat call while fighting and was the first to break away. Squirrel 42 lashed his tail and emitted seven territorial calls in succession. By 1014, the chase still continued, but was interspersed with fights which were becoming increasingly frequent and prolonged.

Now, squirrel 40 emitted defensive threat calls continuously. The interaction was terminated at this point to avoid injury to the squirrel.

While fighting, the squirrels stood on hind legs with heads back, mouths open, and forepaws outstretched. See Fig. 11. The tail was held stiffly vertical, and was flicked rapidly up and down. The forepaws were used for boxing, and occasionally bites were aimed at the head and neck region of the opponent, although the wire barrier prevented bites from making contact. This posture and fighting technique was observed in each fight involving trapped squirrels. There was no apparent postural difference in the two squirrels. The major behavioral differences consisted of their willingness to fight and the types of vocalizations emitted by each.

Next, the cage was moved to an area just inside the boundary of the captive squirrel's territory. About 10 minutes later, squirrel 42 approached the cage very slowly. He paused frequently, watching the captive squirrel in his efforts to escape the cage. At 1029, squirrel 42 emitted the territorial call about 3.5 m from the cage, then began the chase. At 1030, squirrel 40 stopped running and a brief fight occurred, lasting about one second. By 1031, the fighting was continuous, with the captive emitting defensive threat calls and the free squirrel emitting offensive threat

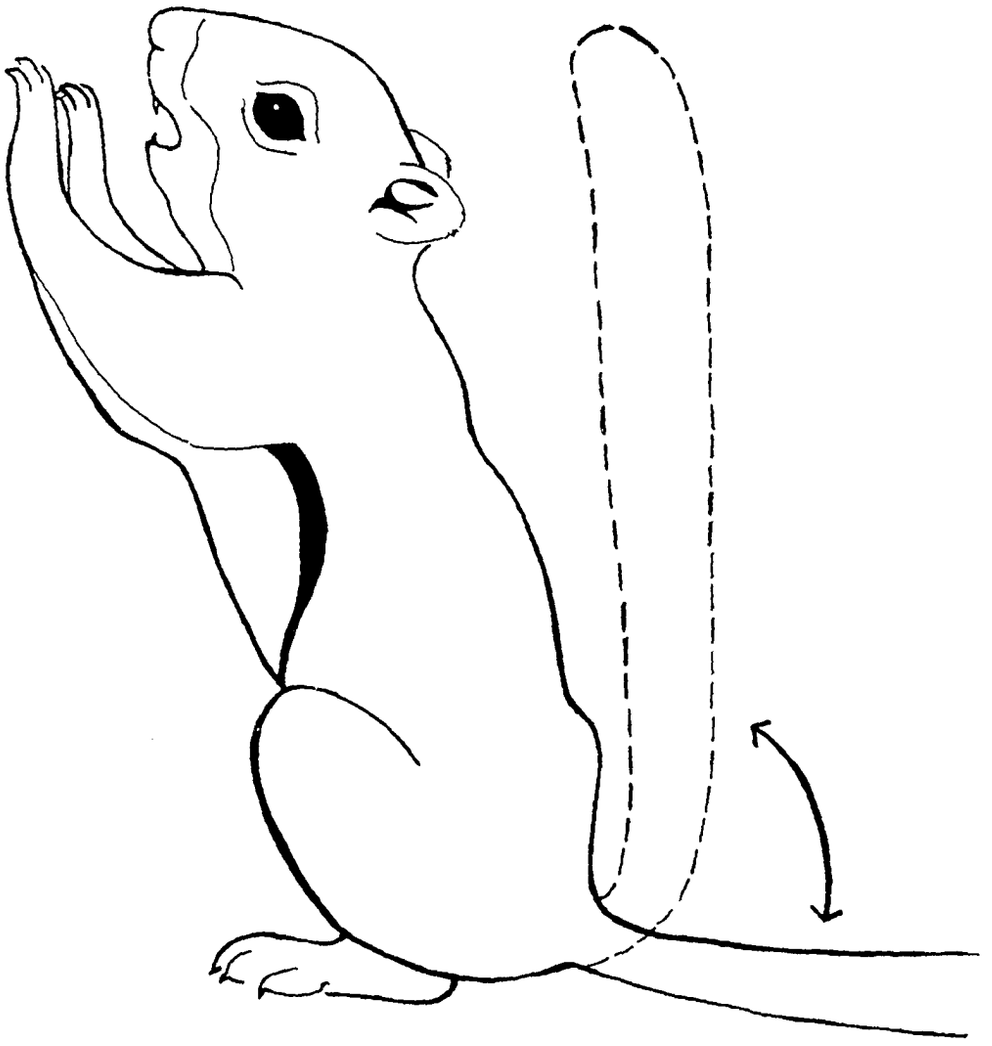

Figure 11. Fighting posture of the red squirrel.

and territorial calls. At this point, the interaction was terminated.

The cage was moved well into the captive's territory, at a point halfway between the boundary and midden 25. The captive squirrel became very calm. He nibbled briefly on a piece of bread, which had been previously ignored. He made attempts to escape, but his efforts were not continuous or as frantic as before. Squirrel 42 emitted a territorial call from the boundary. It was answered immediately by squirrel 40 inside the cage. The free squirrel then retreated to his own midden.

On August 18, 1971, both squirrels were placed in traps on midden 25-BR. The traps were positioned close together, with the sides touching. The squirrels began fighting immediately. This time, both squirrels emitted defensive threat calls. Squirrel 40, the owner of the territory did not emit territorial or offensive threat calls until he was released from the trap after two minutes of fighting. He sprawled on the ground for about a minute resting, then resumed the fight. The aggressive behavior from this point on was similar to that observed during the previous experiment, except that the roles were reversed.

Four other interactions were observed in which invading squirrels entered traps and were discovered by the territorial owner. On June 13, 1971, juvenile male 42 was discovered fighting with his trapped littermate, juvenile male 14,

on midden 4-BR. At that time, squirrel 42 had been defending the midden for less than 24 hours, yet the behavior was identical to that observed in older squirrels. On June 19, 1971, juvenile male 40 was discovered fighting with trapped littermate 28, also a male, on midden 25-BR. Again, the behavior patterns were completely formed. Also on June 19, 1971, adult female 02 fought trapped adult male 17 on her midden, 12-BR. Her behavior was identical to that observed in interactions involving males only. On June 25, 1971, adult male 61 fought with trapped adult male 21 at auxiliary midden 7W-BC. In all four instances, the free squirrel, which normally controlled the territory, emitted territorial and offensive threat calls. The trapped squirrels, all invaders, emitted defensive threat calls only.

On May 19, 1971, adult male 22 was trapped at midden 2-BR, an auxiliary midden on his own territory. Adult male 18 was at midden 3-BR watching the trapped squirrel but not fighting or vocalizing. The middens were about 10 m apart and the boundary fell between them. As soon as squirrel 22 was released, he ran to his own midden, 4. Squirrel 18 followed him almost to midden 4 in what appeared to be a typical territorial chase. This indicates that dominance may indeed be affected by confinement in a trap, for at no point did squirrel 22 leave his territory. He should have assumed dominance, rather than taking flight. C. C. Smith

(1968) reported two instances in which vagrant squirrels were able to defend a territory against its owner after the owner had been confined in a trap for several hours. No such permanent shifts in territory control were observed during the present study. However, traps were checked frequently, and squirrels were seldom confined for longer than a 2-hour period.

On August 3, 1971, a unique interaction was observed at midden 8SW-BC. This midden was being occupied by adult female 01 and her litter, but she did not defend it in any active manner. On this occasion, adult male 19 from midden 3S-BC, was trapped at 8SW. Adult male 55 from midden 3N-BC was running nervously around the trap when I approached for a routine check. The free squirrel charged the trap but stopped short when the trapped animal did not yield. The free squirrel then moved very close, watching as the captive attempted to escape from the trap. He left the area briefly, due to an interruption by the observer, but soon returned running at the trap. A brief fight occurred, lasting about a second. The trapped squirrel emitted the defensive threat call while fighting. The free squirrel ran to a tree 6 m away and began emitting alarm calls. Another charge was attempted, but the trapped squirrel had assumed the fighting posture and was emitting defensive threat calls. Squirrel 55 retreated without following through on the attack. At

this point, squirrel 19 was released. He ran toward the other squirrel. Squirrel 55 fled rapidly to the north, toward his own midden, without pausing to look back. Squirrel 19 remained at 8SW for a short time before moving slowly back to midden 3S. When he reached his midden, he emitted the territorial call. This interaction, occurring on ground neutral to both squirrels differed from previously discussed disputes in three ways. First, the free animal emitted no territorial or offensive threat calls, both calls being very typical of other interactions in which the free squirrel appeared to have the desire to fight but was not able to follow through on most of his aggressive charges. Finally, the confined squirrel was much more aggressive than the other trapped squirrels which were observed. He was not on his own territory, but at the same time, he was not trespassing on another actively defended territory. Perhaps this accounts for his heightened aggressiveness. Possibly, he was just an extremely aggressive squirrel. When he was released, there did in fact seem to be a difference in dominance between the two squirrels. Distance from the home midden may be an important factor here. This distance was twice as far for the subordinate individual.

Establishment of Territories by Juvenile Squirrels

C. C. Smith (1965) observed three red squirrel families

during the period when the juveniles were leaving the nest and establishing their own territories. He found that the young began to explore the area around the nest 7 to 8 weeks after parturition. Two to three weeks after leaving the nest, they were weaned. Typically, the mother moved the young to a weaning nest. The young were permitted free movement within a section of the mother's territory surrounding the new nest, but she defended the rest of her territory from them. Some or all of the young eventually established their territories in the weaning area, which had been formerly controlled by the mother. The young became intolerant of both the mother and their littermates 9 to 11 weeks after birth. C. C. Smith (1968) found that the pattern of territory establishment was variable and attributed it to differences in population density of adult squirrels. Kemp and Keith (1970) found that juveniles left the mother's territory after weaning and dispersed to settle in poorer habitat areas which were not already filled with established territories. The adult females under observation remained on their territories at the time of juvenile dispersal. My observations of territory establishment and the role of the mother are quite different from those described by C. C. Smith and Kemp and Keith. High population pressures coupled with diminishing food supplies in the summer of 1971 may provide the clue to the unusual behavior reported

in this study.

Adult female 02 was observed in a breeding chase on April 1, 1971. She had spent the winter and early spring at midden 1-BR. Throughout April, she gradually shifted her activities to her summer territory, which included auxiliary middens 5, 10, 11, and a much larger midden, 12. The date of parturition was calculated as May 11, 1971, using Layne's (1954) estimated gestation period for the genus Tamiasciurus. The nest was discovered near midden 12 on May 21. On June 9, the juveniles were observed climbing around on the nest tree, only 29 days after birth. By June 14, the young played outside the nest but were not seen to venture far from the nest tree or midden 12. The juveniles were still at midden 12 when observations were suspended on June 23, 43 days after birth. When observations were continued on July 10, 60 days after birth, the nest and midden had been abandoned. According to C. C. Smith's (1968) schedule of events, weaning occurs from 62 to 78 days after parturition. Therefore, the move was probably made before the young were weaned. All the middens on the mother's territory were almost exhausted of cones. It was assumed that the mother and the litter had been forced to move in search of a better food supply. There was no sign of either the mother or the young until August 4, 1971, when the adult female's carcass was discovered at midden 3. The cause of death was not determined. Also, it is not known whether death occurred before or after observations were continued.

There is a possibility that death occurred before July 10, and the young left the territory on their own or starved if they were not ready to be weaned.

Three other families were studied after weaning had occurred. On July 16, 1971, adult female 01 was trapped at 8SW-BC. The ownership of the midden before her arrival is not clear. It appeared to be almost inactive and was being overgrown by grasses and other herbaceous vegetation. It was not, however, completely depleted of old cones. It was probably not controlled by any one squirrel, but was instead at the intersection of several territories. It can be safely assumed that the midden was not controlled by this female before her litter was weaned. She had been tagged as an adult by Krasnowski in 1968. Therefore, she was at least four years old. She was no longer lactating. However, she was still accompanied by four juveniles. They played with her in the vicinity of midden 8SW when she was released from the trap. The mother remained at midden 8SW until July 27, 1971. She made no attempt to defend the midden from four different adult males that visited it, probably attracted by the baited traps. The juveniles were occasionally observed emitting territorial calls from midden 8SW. Their calls did not seem to discourage invaders. Members of the litter were observed at 8SW for a few days after the mother had apparently left the area. On July 23,

an adult female from nearby midden 12W died while being tagged. Juvenile male 69 had become established there by August 3. By August 13, another juvenile from the litter, female 67, gained control of midden 17NE, which had probably been auxiliary to midden 12W before the death of the former owner. Also on August 13, another juvenile was observed at midden 7W. In the early summer, 7W had been an auxiliary midden controlled by an adult male, whose major midden was 1SW-BC. The juvenile was tagged and was subsequently observed at this same midden. It is strongly suspected that he was from the 8SW litter since no other litters of that age were known to be in the area. None of the litter members established a territory at 8SW. On August 27, 1971, no squirrels were observed at the midden. On October 8, 1971, the snow at 8SW was undisturbed by tracks, tunnels, or digging activity.

The post-weaning behavior of the second family was observed at Ballaine Road. The territory containing middens 2 and 4 had been controlled by adult male 22 during the winter and spring of 1971. On the morning of June 12, he was observed at midden 4. That evening, however, he was gone, and a very small juvenile male was emitting an endless succession of territorial calls from the midden. During the next few days, it became obvious that this juvenile, along with three other male litter-mates and the mother had moved into the territory of squirrel 22.

It is not known whether the adult male left his midden under his own initiative. The midden was still well stocked with cones, so he did not leave because of hunger. It is conceivable that the adult female plus her litter could have driven him out by force, but if they did, he probably would have returned to attempt to regain his territory. Therefore, it is assumed that he either left of his own will or else was dead, killed by a predator or other squirrels.

The mother of this second family remained in the grove about one week. She participated in both aggressive and nonaggressive interactions with the juveniles. By the time she left, all but one of the juveniles had become established at their respective territories.

On June 13, 1971, the largest of the litter, squirrel 14, was observed alone on midden 14. On June 16, he was first heard emitting the territorial call at that midden. He successfully controlled it, as well as middens 15, 22, and 26 until October, 1971, when he was forced to leave his territory because the middens were depleted of cones. Squirrel 40, the second largest juvenile, and his litter-mate 28 spent most of their time during the first week near a sack of dog food. On June 19, squirrel 40 chased squirrel 28 from the dog food. The dog food sack was from then on defended in the same manner as a midden. It was designated as midden 25. Squirrel 40 controlled midden 25 until his removal in

March, 1972. Squirrel 28 was not successful in establishing a territory on the study area and was last seen on June 24, 1971, when he was trapped at midden 1.

The smallest member of the litter, squirrel 42 was able to gain control of midden 4. This was probably the most desirable cache in the grove for it was well stocked with white spruce cones. He was the first of the litter to claim his midden. On the evening of June 12, and morning of June 13, he emitted an almost constant succession of territorial calls, pausing only briefly to occasionally strip a cone. At 1033, June 13, his mother appeared on the midden. Both were quiet a few seconds. He then uttered a territorial call, and she began to chase him. During the chase both emitted alarm calls. Finally, he left the midden running east. His mother remained on the midden emitting territorial calls for the rest of that day and all of the next. On June 15, at 1015, juvenile 42 returned to midden 4. He was chased by the female for the next half hour. However, the chase was not as aggressive as that which occurred on June 13. At 1125, the female had left the midden, and juvenile male 42 was there alone emitting territorial calls. At 1530, squirrel 42 and squirrel 40 were playing on midden 4. Nonaggressive chases were interspersed with many pauses, and no vocalizations were heard. After 15 minutes, the mother appeared at midden 4. Juvenile squirrel

40 ran back to midden 25. The mother and squirrel 42 also played together for several minutes before the female left the midden. At 1710, juvenile 40 approached midden 4. Emitting territorial and alarm calls, he began to chase juvenile 42. Squirrel 42 put up no defense but fled, emitting territorial calls. The chase was slow, with many pauses. After 4 minutes of chasing, the smaller squirrel, 42, became the aggressor. The chase then became much faster, with no pauses to nibble cones, etc. At 1720, both squirrels were sitting in trees on opposite sides of the midden. Squirrel 42 ran at his rival. Squirrel 40 jumped to the ground to face him, giving the defensive threat call. However, he did not remain to fight but fled to midden 25. After June 13, squirrel 42 controlled midden 4 until early summer 1972.

The mother was occasionally observed near midden 25 until June 19, 1971. After this date, she was not observed on the study area again.

Territory establishment by the third family occurred in the same grove in 1972. Squirrel 42 was removed from the study area on June 16, 1972. The next day, an adult female and a litter of at least three young squirrels were seen in the area of middens 4-BR and 25-BR alternately playing and disputing over property rights.

In each family, except possibly for female 02 and her litter, my observations indicate that the female actually

left her territory, accompanied by the young, and remained with them until they had established their territories.

Vagrant Squirrels

C. C. Smith (1968) discussed nonterritorial squirrels which he called vagrants. These animals are not vagrant by choice, but represent surplus animals after all the territories have been filled. C. C. Smith described vagrants taking over territories recently vacated by removal of the former occupant. During the present study, it was impossible to determine if a squirrel sighted only once or twice was a vagrant or if it controlled a territory just outside the study area. Red squirrels range far enough from the home territory that the second possibility cannot be ruled out, even if the squirrel was sighted in the center of the study area.

Probably most vagrants in the autumn are juveniles which have not yet discovered a vacant territory in which to settle. The probability of a vagrant squirrel surviving the coldest portion of the winter in interior Alaska is unknown. After the snow falls, vagrants probably obtain most of their food by raiding other middens. During the coldest weather (below $-34^{\circ}C$) territorial squirrels do not normally range far from the midden. Thus in a situation like that at Bonanza Creek, where each territorial squirrel controls one midden, the opportunities to raid middens are greatly

decreased during these cold periods. A vagrant probably would have greater survival chance during the critical winter months at Ballaine Road. There, auxiliay middens are far-flung and rarely visited by the territorial owner when temperatures are low. Thus, a vagrant squirrel could conceivably settle for a short period at one of these auxiliary middens during the winter.

Kemp and Keith (1970) observed that those squirrels which were not able to obtain prime territories in coniferous habitats defended winter food caches consisting primarily of nuts from hazel Corylus cornuta shrubs in deciduous areas. They felt that all squirrels must be territorial, at least in the winter, or face almost certain starvation. During the summer, when food was plentiful, the squirrels which defended winter caches became free-ranging and competed for prime territories in the coniferous areas.

In the spring of 1972, many untagged squirrels were observed moving through the Ballaine Road study area. Such large scale movement did not occur in the spring of 1971. It is possible that some of these animals had survived the winter as vagrants. Most of them were probably territorial squirrels which were forced to leave their territories when the middens became exhausted. Some of these vagrants could have wintered in adjacent deciduous stands. At present, the extent to which red squirrels utilize such habitats in interior Alaska is poorly known.

CONCLUSIONS

The food habits study of free-ranging squirrels at the Ballaine Road study area supports the experimental results obtained by Brink (1966), showing preference of white spruce cones as food source. It should be noted that black spruce was readily cut by many squirrels in 1971 when white spruce cones were not available. However, in 1970, when white spruce cones were present, they were chosen and black spruce cones were generally ignored. Although some black spruce cones were cut by two squirrels in 1970, they were not consumed until late summer, 1971, when white spruce cones were nearly gone. Also, when squirrels raided neighboring middens in the autumn of 1971, they repeatedly ignored the piles of black spruce and instead dug for white spruce cones.

Evidence from both study areas indicates that adult squirrels and possibly males controlled the more desirable middens. Also, the adults cached greater quantities of cones.

The basic drive to cache is probably instinctive. Most juveniles are self-sufficient when the cone harvest begins. The three components of caching behavior: cutting, transport to the midden, and burial of cones can all be performed by juvenile squirrels.

The more efficient performance of the adults can be accounted for in two ways. First, juvenile squirrels may acquire greater efficiency through learning. Secondly, only those juveniles that perform above some minimum level of efficiency survive the first winter. The fact that two juveniles at Ballaine Road managed to survive the first winter even though they cached no cones suggests that the second premise can be circumvented by alternate and less frequent behavior patterns. It would be of interest to follow the development of caching behavior of several marked squirrels throughout their lifespan to determine the exact role that learning plays.

The positive correlation of preharvest food supply in the midden and the number of years the midden has been active may be the result of purely physical factors or of social factors. As mentioned previously, long term use enhances the properties of middens as areas of cone storage. Also, certain middens may be used frequently and contain greater stores of cones because of proximity to particularly productive trees. However, I would hypothesize that social factors can assume overriding importance if squirrels of particular age and sex classes traditionally control certain middens. The greater or lesser caching activity of these animals may have caused the differences in food levels in the middens. Also, competition for territories containing

especially productive trees may result in the control of these middens by certain age and sex classes.

Seven different vocalizations were distinguished during the course of this study. Territorial calls are associated with defense and marking of the territory. They are emitted without apparent external stimuli to announce the presence of the owner on the territory. Although it is used primarily during intraspecific interactions, the call is emitted any time a squirrel attempts to drive a nonpredatory animal from the area of the midden.

The alarm call is quite complex, both in structure and function. It could serve to cause a response by the object which stimulates the call. This response would then help the squirrel to identify the object if it were a predator. Also, it may have the function of relieving tension caused by fear, frustration, or surprise. The alarm call is probably not altruistic in nature.

Two aggressive calls were recognized. The offensive threat call relates to territorial defense and is emitted by the dominant squirrel during territorial chases and boundary disputes. It is often emitted directly before or after the territorial call. The defensive threat call seems to communicate aggressive intent of a squirrel being forced into a position of subordinance.

Three types of appeasement calls were recognized. The buzz has been well documented in the literature (Layne, 1954;

Hazard, 1960; C. C. Smith, 1965), probably because of its peculiar sound, which makes it quite noticeable, and its association with the boisterous mating chases which are commonly seen by even the casual observer. C. C. Smith (1965) observed that its function was broader than that of a mating call and named it the appeasing call. He felt that the call signified nonaggressive intent toward other squirrels. The second appeasement call, the whimper, was emitted by juvenile squirrels and appeared to inhibit aggressive behavior by adult squirrels. The third appeasement call, consisting of a series of soft squeaks, seemed to communicate not only a lack of aggressive intent but also a willingness to participate in close physical contact, such as play behavior.

Territorial behavior, centering around the midden, is the mechanism by which the red squirrel protects its food supply from neighboring and vagrant squirrels. Until information is gathered concerning the percentages of vagrant versus territorial squirrels, we can only hypothesize about the role of territorial behavior in regulating the population and/or breeding stock densities. Those percentages probably vary from year to year because of fluctuations in food supply and population densities. Kemp and Keith (1970) found the percentage of prime territorial squirrels to be 31% in 1967 and 26% in 1968 on two study areas containing both deciduous and coniferous habitat. Red squirrel studies in interior

Alaska have concentrated on coniferous habitats, where squirrels defend prime territories on a year round basis. Utilization of deciduous stands by Alaskan red squirrels should be examined in the future to see how over-winter survival in these areas affects population dynamics.

Squirrels will readily invade a neighboring territory during the absence of the owner. When the owner is present, the territorial call seems to be an effective deterrent to invasion. Some of the incidents described in the results show that the presence of the owner of the territory does not automatically cause an invader to assume a position of subordinance. Other factors such as age, size, or the relative aggressiveness of each individual are important factors in determining whether an invader will fight or flee. Since only males were involved in these interactions, it is not possible to draw any conclusions concerning the dominance of one sex over the other.

There are two major functions of the boundary dispute, first, it serves to define the boundary clearly. The establishment of a boundary does not eliminate all aggressive contacts from that point on, and other boundary disputes will probably occur. The boundary dispute does, however, serve to eliminate continuous friction. Where middens are farther apart, the boundary is probably ephemeral at best. Secondly, boundary disputes allow a squirrel to evaluate his neighbor. The relative age, size, or aggressiveness of the two squirrels

will determine where the boundary falls. Furthermore, this opportunity to examine the neighbor's strengths and weaknesses probably influences a squirrel's motivation to trespass on the neighbor's territory.

Territorial squirrels fight trapped invaders with no hesitation and are very aggressive. Fighting will occur if the trap is placed at any point on the regularly defended territory, and may even occur when the trap is just outside the territorial boundary of the free squirrel. No age or sex differences in behavior were observed among several squirrels under similar circumstances, i.e. invader in trap, owner free. These interactions are highly artificial, since under more natural conditions, invaders usually flee without attempting to fight. Fighting between free-ranging squirrels was observed only once, and the fight lasted only a couple of seconds. In this brief contact, the fighting posture was similar to that observed during interactions involving trapped squirrels. This indicates that the vertical fighting posture was not an artifact caused by the presence of the vertical barrier of the cage wall. Even though these interactions are artificial, they add to our understanding of territorial defense and aggression in the red squirrel. The last interaction discussed demonstrates that aggressive behavior occurs even when both the trapped and untrapped individuals are on neutral ground. Territorial

defense was not a factor, nor was competition for a mate or food. The free squirrel had ready access to any cones he could find on the midden, and it was unnecessary to harass the trapped animal. Competition for the trap and bait was not a factor, for there was another baited trap on the same midden. The basic response when sighting another squirrel is probably an aggressive one. This response is modified by the location, behavior, age, size, and vocalizations of the other squirrel. It is also modified by the sex of the squirrel during the breeding season. If the squirrel is trespassing, the response of the owner will be defense of the territory, which involves chasing and emission of territorial calls. If the invader proves to be a female in estrous, or if the squirrel emits an appeasing call, the response of the owner may be modified and trespass tolerated. Also, if the invader is larger, older, and aggressive, the owner may be forced to assume a more subordinate role. If a squirrel is not on his own territory, he will also respond aggressively to another squirrel. This response is modified if the other squirrel demonstrates control of the territory by emitting the territorial call. The call curbs aggression and elicits a flight response, unless the owner is considerably younger, smaller, or seems reluctant to attack or chase. This model presents a highly simplistic view of territorial defense and aggression but is helpful in explaining the interactions observed during this study.

My observations of the role the mother plays in establishment of territories by juvenile squirrels are quite different from those described by previous workers. My observations were limited to only four families, but in each case, except possibly for one, the mother actually left her own territory accompanied by the litter. As mentioned earlier, the poor food supply and high population pressures in the summer of 1971 might have prompted this apparently unusual behavior. Also, the female of the last family discussed had gone through the winter of 1971-72 following the complete failure of the 1971 cone crop. One would expect the midden of a female with young to be more rapidly depleted than the middens of males and barren females. Thus, perhaps by the time the young were weaned, the mothers may have been forced to leave their territories to seek new food supplies. The fact that the middens controlled by female 02 were depleted when the territory was vacated supports this argument. In the other three cases, the families happened upon areas recently vacated or poorly defended by other squirrels. With the exception of the aggressive encounters between juvenile 42 and his mother, the females were not observed helping or hindering the process of territory establishment by their offspring. They did, however, remain in loose association with the juveniles until establishment or shortly before establishment of territories by the juveniles was accomplished.

APPENDIX A

Squirrels Trapped on the Bonanza Creek and Ballaine Road Study Areas

Bonanza Creek Experimental Forest

Tag Number	Abbreviated Number Used in Text	Age	Sex
3701-3318	01	adult	female
3319-3320	19	adult	male
3321-3322	21	adult	male
3329-3330	29	adult	male
3333-3334	33	juvenile	male
3335-3336	35	adult	male
3337-3338	37	juvenile	female
3347-3348	47	adult	male
3349-3350	49	adult	female
3351-3352	51	juvenile	female
3353-3354	53	adult	male
3355-3332	55	adult	male
3357-3358	57	adult	female
3359-3360	59	adult	female
3361-3362	61	adult	male
3363-3364	63	adult	male
3365-3366	65	juvenile	female
3367-3368	67	juvenile	female
3369-3370	69	juvenile	male
3373-3374	73	adult	male

Tag Number	Abbreviated Number Used in Text	Age	Sex
3375	75	juvenile	male
3378-3379	78	adult	female
3382-3383	82	adult	male
3384-3385	84	?	female
3386-3387	86	?	male
3388-3389	88	?	male

Ballaine Road Study Area

Tag Number	Abbreviated Number Used in Text	Age	Sex
3301-3302	02	adult	female
3305-3306	06	adult	female
3307-3308	08	adult	female
3309-3310	10	juvenile	male
3311-3312	12	adult	male
3713-3714	13	adult	male
3313-3314	14	juvenile	male
3715-3716	15	adult	female
3315-3316	16	adult	female
3303-3317	17	adult	male
3717-3718	18	adult	male
3721-3722	22	adult	male
3327-3328	28	juvenile	male
3339-3340	40	juvenile	male
3341-3342	42	juvenile	male

Tag Number	Abbreviated Number Used in Text	Age	Sex
3343-3344	44	adult	female
3371-3372	72	adult	male
3345-3376	76	juvenile	female
3380-3381	81	adult	male

APPENDIX B

The accompanying tape illustrates four red squirrel vocalizations. Included are examples of the territorial call, the alarm call, the defensive threat call, and the offensive threat call. The tape should be played at the speed of 7.5 inches per second.

LITERATURE CITED

American Ornithologist's Union. 1957. Check-list of North American birds. 5th Ed. Lord Baltimore Press, Inc., Baltimore, Md. 691 p.

Brink, C. H. 1964. Spruce seed as a food of the squirrels Tamiasciurus hudsonicus and Glaucomys sabrinus in interior Alaska. M. S. Thesis. Univ. of Alaska, College. 7

_____, and F. C. Dean. 1966. Spruce seed as a food of red squirrels and flying squirrels in interior Alaska. J. Wildl. Mgmt. 30(3):503-512.

Finley, R.B. 1969. Cone caches and middens of Tamiasciurus in the rocky mountain region. Contributions in Mammalogy. Univ. of Kansas Mus. Nat. Hist. Misc. Publ. 51. 428 p.

Fitzwater, W. D., Jr. 1941. The red squirrel: territorialism, activity, census methods. M. S. Thesis. New York State College of Forestry, Syracuse. 117 p.

Hall, E. R. and K. R. Kelson. 1959. The mammals of North America. 2 vols. The Roland Press Company, N. Y. 1,083 p.

Hazard, E. B. 1960. A field study of activity among squirrels (Sciuridae) in southern Michigan. Ph.D. Thesis, Univ. of Mich. (Libr. Congr. Card No. Mic. 60-2536). 281 p. Univ. Microfilms, Ann Arbor, Mich. (Diss. Abstr. 21:379-380.)

Kemp, G. A. and L. B. Keith. 1970. Dynamics and regulation of red squirrel (Tamiasciurus hudsonicus) populations. Ecology 51(5):763-779.

Krasnowski, P. V. 1969. Aspects of red squirrel (Tamiasciurus hudsonicus) population ecology in interior Alaska. M. S. Thesis. Univ. of Alaska, College. 63 p.

Layne, J. N. 1954. The biology of the red squirrel, Tamiasciurus hudsonicus loquax (Bangs), in central New York. Ecol. Monog. 24(3):227-267.

LeBarron, R. K. 1948. Silvicultural management of black spruce in Minnesota. U.S. Dep. Agric. Circ. 791. 60 p.

Modafferi, M. M. 1972. Aspects of the reproductive biology of the red squirrel (Tamiasciurus hudsonicus) in interior Alaska. M. S. Thesis. Univ. of Alaska, College. 82 p.

Smith, C. C. 1965. Interspecific competition in the genus of tree squirrels Tamiasciurus. Ph.D. Thesis. Univ. of Wash., Seattle. 269 p.

_____. 1968. The adaptive nature of social organization in the genus of tree squirrels Tamiasciurus. Ecol. Monog. 38:31-63.

Smith, M. C. 1967. Red squirrel (Tamiasciurus hudsonicus) ecology during spruce cone failure in Alaska. M. S. Thesis. Univ. of Alaska, College. 68 p.

_____. 1968. Red squirrel responses to spruce cone failure in interior Alaska. J. Wildl. Mgmt. 32(2): 305-316.

Streubel, D. P. 1968. Food storing and related behavior of red squirrels (Tamiasciurus hudsonicus) in interior Alaska. M. S. Thesis. Univ. of Alaska, College. 56 p.

Viereck, L. A. and E. L. Little, Jr. 1972. Alaska trees and shrubs. U.S. Forest Serv., Agriculture Handbook No. 410. 265 p.

Werner, R. A. 1964. White spruce seed loss caused by insects in interior Alaska. Canad. Ent. 96(11): 1462-1464.

Zasada, J. C. 1971. Natural regeneration of interior Alaska forests - seed, seedbed, and vegetative reproductive considerations. Pages 231-246 in

C.W. Slaughter, R. J. Barney and G. M. Hansen, eds. Fire in the northern environment - a symposium. U.S. Forest Serv., Pacific Northwest Forest and Range Experimental Station., Portland, Ore. 275 p.

_____, and L. A. Viereck. 1970. White spruce cone and seed production in interior Alaska, 1957-68. U.S. Forest Serv., Pacific Northwest Forest and Range Experimental Station, Research Note 129. 11 p.